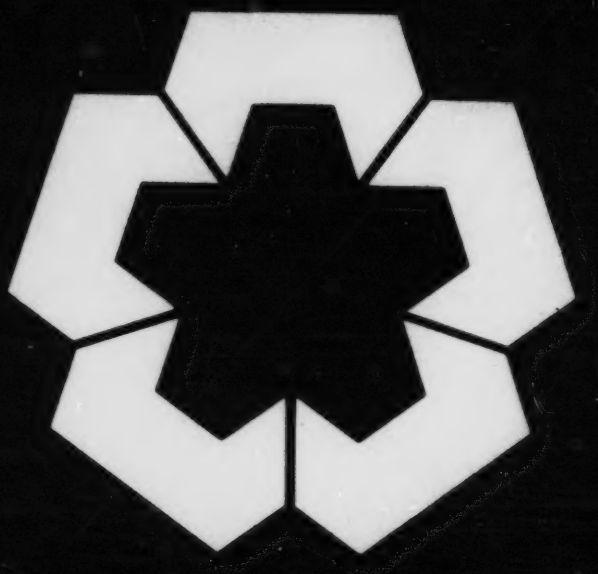

The Influence of Phosphorus And Zooplankton On Chlorophyll Levels In Alberta Lakes

K.H. Mathias

Alberta

The logo represents the interdisciplinary and holistic nature of the Division's environmental research programs. Each of the five sections of the symbol represent comprehensive programs on air, water, land, humans, and their constant interaction. The sections converge to form a cohesive chain, characteristic of an effective research organization. This cohesive bonding makes the sections blossom into the environment in the form of a flower — an Albertan wild rose.

THE INFLUENCE OF PHOSPHORUS AND ZOOPLANKTON ON CHLOROPHYLL LEVELS IN ALBERTA LAKES

RESEARCH MANAGEMENT DIVISION
Alberta Environment

For further information on reports published by the Research Management Division, contact:

Research Management Division
14th Floor, Standard Life Centre
10405 Jasper Avenue
Edmonton, Alberta
T5J 3N4

(403) 427-3946

This report may be cited as:

Prepas, E.E. 1983. The influence of phosphorus and zooplankton on chlorophyll levels in Alberta lakes. Prep. for Alberta Environment, Research Management Division by Department of Zoology, University of Alberta. Edmonton, Alberta: Research Management Division. RMD Report 83/23. 111 pp.

THE INFLUENCE OF PHOSPHORUS AND ZOOPLANKTON ON CHLOROPHYLL LEVELS IN ALBERTA LAKES

by

E.E. PREPAS

Department of Zoology
University of Alberta

for

RESEARCH MANAGEMENT DIVISION
Alberta Environment

RMD Report 83/23

August 1983

This report is made available as a public service. The Department of Environment neither approves nor disagrees with the conclusions expressed herein, which are the responsibility of the author.

TABLE OF CONTENTS

		Page
LIST OF TABLES		vi
LIST OF FIGURES		viii
ABSTRACT		ix
ACKNOWLEDGEMENTS		x
1.	INTRODUCTION	1
1.1	The Phosphorus–Chlorophyll Relationship in Alberta	1
1.2	Seasonal Dynamics of Total Phosphorus in Alberta Lakes	2
1.3	The Influence of Large Zooplankton on the Chlorophyll Biomass in Alberta Lakes	3
2.	MATERIALS AND METHODS	4
2.1	The Study Lakes	4
2.2	Sample Collection and Analysis	4
2.3	Physical Data on the Lakes	4
2.4	Sampling Regime	7
2.5	Sample Analyses	9
3.	GENERAL CHARACTERISTICS OF THE STUDY LAKES	13
4.	PHOSPHORUS–CHLOROPHYLL MODELS	16
4.1	The Inputs to the Phosphorus–Chlorophyll Models	16
4.2	Phosphorus–Chlorophyll Relationships in Alberta Lakes	17
4.3	Nitrogen–Chlorophyll Relationship in Alberta Lakes	22
4.4	Discussion of Phosphorus–Chlorophyll Model	22
5.	TOTAL DISSOLVED SOLIDS AS A PREDICTOR OF LAKE BIOMASS AND PRODUCTIVITY IN ALBERTA LAKES	25
6.	SEASONAL DYNAMICS OF TOTAL PHOSPHORUS IN ALBERTA LAKES	29
6.1	The Lakes Used in This Study	29
6.2	Shallow Lakes	29
6.3	Deep Lakes Where the Euphotic Zone Did Not Extend into the Hypolimnion	31
6.4	Deep Lakes Where the Euphotic Zone Extended into the Hypolimnion	33
6.5	Phosphorus–Nitrogen–Chlorophyll Relationships	37
6.6	Sediments as a Phosphorus Source	37
7.	THE IMPORTANCE OF LARGE ZOOPLANKTON IN THE TOTAL PHOSPHORUS POOL	43
7.1	Calibration of 250-μm Tow Nets	43
7.2	Phosphorus in the > 250 μm Fraction	45
7.3	Phosphorus–Chlorophyll Relationship and PP > 250 μm	65
7.4	Discussion	69
8.	SUMMARY OF THE INFLUENCE OF PHOSPHORUS AND ZOOPLANKTON ON CHLOROPHYLL LEVELS IN ALBERTA LAKES	71
9.	REFERENCES CITED	73
10.	APPENDIX	81

LIST OF TABLES

		Page
1.	Background Data for the 29 Study Lakes	5
2.	Nutrient and Chlorophyll Data and the Thermal Characteristics for the 27 Lakes Studied in 1980 and 1981	14
3.	A Comparison of Total Phosphorus Concentrations Reported by Gallup and Hickman and Data Collected in This Study in 10 Alberta Lakes	23
4.	Relationships between Total Dissolved Solids and Indices of Productivity from Reports Which Include Lakes Both on and off the Precambrian Shield	27
5.	Ratio of Total Dissolved Phosphorus to Total Phosphorus in the Epilimnion of 11 Lakes in Central Alberta	34
6.	Increase in Total Phosphorus in the Hypolimnion of Four Deep Lakes, during the Summer 1982	35
7.	Average Ratio of Total Nitrogen to Total Phosphorus in the Epilimnion of the Lakes Studied in Central Alberta in 1982	38
8.	Correlations between Total Phosphorus, Total Nitrogen, and Chlorophyll *a* concentrations in the Euphotic Zone of the Study Lakes	39
9.	Vertical Distribution of Total Dissolved Phosphorus in Bob Lake, 1978	41
10.	Ratios of Particulate Phosphorus > 250 µm Collected by the Schindler–Patalas Trap to That Collected by a Tow Net in Nine Lakes in Central Alberta	44
11.	Ratios of Particulate Phosphorus Collected by Tow Nets Made with 250– and 80–µm Mesh	46
12.	Vertical Variation in Particulate Phosphorus > 250 µm in 1980 in Eight Lakes in Central Alberta	47
13.	Particulate Phosphorus in the Fraction > 250 µm and Percent of the Total Phosphorus Pool in the Fraction > 250 µm in the Euphotic Zone of the 15 Lakes Studied in 1981	54
14.	Particulate Phosphorus in the Fraction > 250 µm and in the Animal Portion of This Fraction and Percent of the Total Phosphorus Pool in the Fraction > 250 µm in the Euphotic Zone of the 12 Lakes Studied in 1982	58
15.	Percent of the Total Phosphorus Pool in the Entire Fraction > 250 µm and in the Animal Portion of This Fraction for 17 Lakes in Central Alberta Which Were Sampled in 1981 and 1982	63
16.	Spring Total Phosphorus (TP) and Summer TP and Summer Chlorophyll *a* Collected in 1982 in 12 Alberta Lakes	64
17.	Temperature Profiles for Amisk N. Lake, 1982	82
18.	Temperature Profiles for Amisk S. Lake, 1982	83
19.	Temperature Profiles for Baptiste N. Lake, 1982	84
20.	Temperature Profiles for Baptiste S. Lake, 1982	85

Page

21. Temperature Profiles for Eden Lake, 1982. 86
22. Temperature Profiles for Hasse Lake, 1982. 87
23. Temperature Profiles for Lessard Lake, 1982. 88
24. Temperature Profiles for Mink Lake, 1982. 89
25. Temperature Profiles for Peanut Lake, 1982. 90
26. Temperature Profiles for Sauer Lake, 1982. 91
27. Temperature Profiles for Twin Lake, 1982. 92
28. Temperature Profiles for Wizard Lake, 1982. 93
29. Vertical Profiles of Total Phosphorus at Amisk N. Lake, 1982. 94
30. Vertical Profiles of Total Phosphorus at Amisk S. Lake, 1982. 95
31. Vertical Profiles of Total Phosphorus at Baptiste N. Lake, 1982. . . . 96
32. Vertical Profiles of Total Phosphorus at Baptiste S. Lake, 1982. . . . 97
33. Vertical Profiles of Total Phosphorus at Eden Lake, 1982. 98
34. Vertical Profiles of Total Phosphorus at Hasse Lake, 1982. 99
35. Vertical Profiles of Total Phosphorus at Lessard Lake, 1982. 100
36. Vertical Profiles of Total Phosphorus at Mink Lake, 1982. 101
37. Vertical Profiles of Total Phosphorus at Peanut Lake, 1982. 102
38. Vertical Profiles of Total Phosphorus at Sauer Lake, 1982. 103
39. Vertical Profiles of Total Phosphorus at Twin Lake, 1982. 104
40. Vertical Profiles of Total Phosphorus at Wizard Lake, 1982. 105
41. Average Chlorophyll *a* in the Euphotic Zone of 12 Study Lakes for Each Sampling Date in 1982. 106
42. Average Total Nitrogen in the Euphotic Zone of 12 Study Lakes for Each Sampling Date in 1982. 107
43. Zooplankton Species Found in Select Samples from 19 Lakes in Central Alberta. 108

LIST OF FIGURES

		Page
1.	Relationship Between Mean Summer Chlorophyll and Total Phosphorus at Spring Overturn in Lakes in Central Alberta	18
2.	Total Phosphorus Concentration in the Euphotic Zone of a Shallow Lake, Nakamun, and a Deep Lake, Twin, from May until August 1980	20
3.	Relationship between Summer Chlorophyll *a* within the Euphotic Zone and Total Dissolved Solids within the Epilimnion in 27 Lakes in Central Alberta in 1981 and 1982	26
4.	Temporal Variation in the Vertical Distribution of Temperature and the Concentration of Total Phosphorus in the Euphotic Zone of Four Shallow Lakes in Central Alberta in 1982	30
5.	Temporal Variation in the Vertical Distribution of Temperature and the Concentration of Total Phosphorus in Four Deep Lakes in Central Alberta in 1982	32
6.	Temporal Variation in Temperature and the Concentration of Total Phosphorus in Four Lakes in Central Alberta in 1982	36
7.	Vertical Distribution of Particulate Phosphorus > 250 µm and Temperature in Amisk N. Lake, 1980	51
8.	Vertical Distribution of Particulate Phosphorus > 250 µm and Temperature in Hubbles Lake, 1980	52
9.	Vertical Distribution of Particulate Phosphorus > 250 µm, Chlorophyll *a*, Total Phosphorus < 250 µm, and Temperature in Amisk N. Lake, 1981	56
10.	Vertical Distribution of Particulate Phosphorus > 250 µm, Chlorophyll *a*, Total Phosphorus < 250 µm, and temperature in Hubbles Lake, 1981	57
11.	Temporal Variation in the Concentration of Total Phosphorus < 250 µm, Chlorophyll *a*, and Particulate Phosphorus in Animals > 250 µm in Three Lakes in Central Alberta in 1982	61
12.	Relationship Between Percent of the Total Phosphorus Pool in Particulate Phosphorus > 250 µm and the Deviations of the Predicted Concentration of Chlorophyll *a* Based on Spring Concentration of TP < 250 µm and Observed Chlorophyll in 15 Lakes in Central Alberta in 1981	67
13.	Relationship Between Percent of the Total Phosphorus Pool in the Animal Portion of Particulate Phosphorus > 250 µm and the Deviations of the Predicted Concentration of Chlorophyll a Based on Spring Concentration of TP < 250 µm and Observed Chlorophyll in 12 Lakes in Central Alberta in 1982	68

ABSTRACT

Data were collected on 20 lakes in central Alberta to determine if: (1) local lakes are phosphorus-limited; (2) predictable patterns exist in the return of phosphorus from the sediments; and (3) including an estimate of zooplankton biomass would improve the phosphorus-chlorophyll models for local lakes. The first part of this study was carried out in conjunction with D.O. Trew, Alberta Environment, Water Quality Control Branch.

Contrary to previous studies in western Canada, it was found that both the total phosphorus (TP)-chlorophyll *a* (Chl *a*) relationship and the total nitrogen (TN) to TP ratios were similar to those reported for other northern temperate lakes which are considered phosphorus limited. However, more variability in the spring TP-summer Chl relationship was found than reported elsewhere. This variation was caused by unexpectedly large seasonal fluctuations in TP levels in the surface waters.

Temporal variations (May to Sept.) in TP were dependent on the amount of phosphorus released from the sediments and on mixing depth. In shallow lakes (i.e., those which mix intermittently), [TP] in the surface waters increased during the summer period. The shallow lakes stratified intermittently and, during these periods, the [TP] in the water above the sediments increased as dissolved oxygen levels approached zero. Later, when the lake mixed, this phosphorus was incorporated into the surface waters. The deep lakes (i.e., those which are permanently thermally stratified during summer) were all partially meromictic, and [TP] increased in the hypolimnion during summer. The rate of phosphorus release from the sediments of deep lakes was correlated with mean summer [Chl *a*]. This hypolimnetic phosphorus pool was either primarily dissolved or particulate, depending on the relative depth of the euphotic zone. During the summer period, the [TP] in the surface waters of the deep lakes stayed constant or declined, except in late summer when the thermocline was depressed and dissolved phosphorus had accumulated at the top of the hypolimnion.

An estimate of the large zooplankton biomass improved the spring TP-summer Chl *a* relationship for local lakes. However, this term did not improve the summer TP-summer Chl *a* relationship in the same lakes. These apparently contradictory results can be explained by the differences in the ratio of summer TP to spring TP and percent of TP pool in PP > 250 μm in shallow and deep lakes.

ACKNOWLEDGEMENTS

The author expresses thanks to the Research Management Division of Alberta Environment, Alberta Environmental Research Trust, and the Natural Sciences and Engineering Research Council of Canada for funding this research project; J. Vickery for assistance in every aspect of the report; D.O. Trew, Alberta Environment, Water Quality Control Branch, for co-operating in a major portion of this project in 1981; G. Hutchinson, for excellent assistance with analytical work; K. Luco, L. Jorgenson, and I. Wisheu for long hours spent in the field and assistance with analytical work; P.A. Murtaugh for identifying the zooplankton in the study lakes; J. Babin, M. Herdman, and E. Riley for providing unpublished morphometric data; H. Hamilton and T. Reynoldson, Alberta Environment, Water Quality Control Branch, for providing unpublished phosphorus data; J. Scheinas for typing the manuscript; and T. Reynoldson, H. Hamilton, P. Mitchell, and D.O. Trew, Alberta Environment, Water Quality Control Branch, for supporting this project.

The results reported in Sections 4 and 5 have been published in the Canadian Journal of Fisheries and Aquatic Sciences (Vol. 40: 27-35; Vol. 40: 92-95). The results reported in Sections 6 and 7 have been submitted to the same journal.

1. INTRODUCTION

1.1 THE PHOSPHORUS–CHLOROPHYLL RELATIONSHIP IN ALBERTA

The proportionality of phytoplankton biomass and productivity to total phosphorus concentration ([TP]) has been documented in many limnological studies (Nicholls and Dillon 1978; Smith 1979) and forms the basis of eutrophication control schemes (Dillon and Rigler 1975). This relationship between phytoplankton biomass and [TP] is robust, except in lakes with low ratios of total nitrogen (TN) to TP (e.g., Sakamoto 1966), although the definition of a low TN to TP ratio (by weight) varies from 5 (Schindler 1977) to 13 (Smith 1979). However, data collected on lakes in western Canada suggest that they are nitrogen– rather than phosphorus–limited (Allan and Kenney 1978; Gallup 1978; Hickman 1980). Thus, if the data are correct, management models based on phosphorus would be inappropriate for Alberta lakes, leaving Albertans without an important tool for lake management.

To re–evaluate the TP–chlorophyll (Chl) relationship in Alberta, data on [TP], [TN] and [Chl *a*] for 25 lakes in central Alberta were collected in conjunction with Alberta Environment, Water Quality Control Branch, during 1980 and 1981. An additional purpose was to compare the TP–Chl relationship in this study with those reported for other temperate lakes to assess whether Alberta lakes were phosphorus–limited (Schindler 1977). From numerous models (see Table 1 in Nicholls and Dillon 1978), the relationship found by Dillon and Rigler (1974a) was chosen because it was based on a broad range of lakes and used data collected only from May through August.

Contrary to the results reported in the previous studies in western Canada, the spring TP–summer Chl relationship (n = 29, r^2 = 0.67) and TN to TP ratios in our study were similar to those reported for other northern temperate lakes. However, there was more variability in the spring TP–summer Chl relationship than reported elsewhere. This variation was caused by unexpectedly large seasonal fluctuations in TP levels in the surface waters.

1.2 SEASONAL DYNAMICS OF TOTAL PHOSPHORUS IN ALBERTA LAKES

The seasonal variation in [TP] in lakes is not well understood. Some unproductive and moderately productive lakes have very little temporal variation in [TP] in the surface waters (e.g., Candice Lake, New York, [Stewart and Markello 1974]; Horw Bay, Switzerland, [Bloesch et al. 1977]; Bob Lake, Ontario, [Prepas and Rigler 1982]). In addition, the small amount of seasonal variation is predictable for many lakes (Chapra and Tarapchak 1976; Nicholls and Dillon 1978). This small and predictable seasonal variation is useful in the development of lake management models (e.g., Dillon and Rigler 1974b). However, in other lakes, [TP] in the surface waters varies considerably during the open-water period (e.g., Shagawa Lake, Minnesota [Larsen et al. 1975]; Rotsee, Switzerland [Bloesch et al. 1977]). Lakes with highly variable TP levels are difficult to model and, thus, manage because the factors controlling seasonal pulses are not well understood.

In central Alberta, the [TP] varies considerably in the surface waters of most lakes (Prepas and Trew 1983). It was found that the [TP] in the surface waters of shallow lakes (i.e., those which mix intermittently in summer) was often two-to-three times higher in summer than in spring. In contrast, in the deep lakes (i.e., those which are permanently thermally stratified in summer) summer TP values were half of the spring values. The water overlying the sediments in Alberta lakes was frequently anoxic in the shallow lakes and nearly always anoxic in the deep lakes. Under reducing conditions, phosphorus is highly soluble and is released from lake sediments (Holdren and Armstrong 1980). Thus, the seasonal variation in TP in Alberta lakes could be linked to exchanges between the sediments and open water.

To collect more complete data on seasonal fluctuations in TP and to evaluate the role of sediment release in these fluctuations, 12 lake basins in central Alberta were monitored. Concentrations of TP, TN, and Chl *a* were measured in the euphotic zone from ice-out in May until late September in 1982. In addition, the vertical distribution of TP was measured in the deep lake basins.

1.3 THE INFLUENCE OF LARGE ZOOPLANKTON ON THE CHLOROPHYLL BIOMASS IN ALBERTA LAKES.

There are suggestions in the literature that the large zooplankton can regulate the size of the phytoplankton community (Shapiro et al. 1975; Burgi et al. 1979; Lynch and Shapiro 1981; Hoyer and Jones 1982). These observations prompted Harris (1980) to postulate that some of the residual variation in the TP–Chl *a* models is due to the relative size of the zooplankton community. Since there is considerable variation in the TP–Chl *a* relationship for Alberta lakes, the present study investigated whether the relative importance of the large zooplankton biomass could explain some of this variation.

The large zooplankton biomass was estimated as particulate phosphorus (PP) > 250 µm since PP > 250 µm was mainly large zooplankters in the one lake investigated (Prepas and Rigler 1982). Although the general importance of PP > 250 µm in lake water samples is unknown, it formed a significant portion of the TP pool in Prepas and Rigler's study. However, PP > 250 µm is usually measured inaccurately or ignored in lake water samples (Prepas and Rigler 1982). An improved assessment of this fraction of the TP pool could result in better estimates of lake TP and possibly better lake management models.

To evaluate the general importance of PP > 250 µm, data were collected on both the seasonal and vertical distribution of this fraction over three years in a total of 15 lakes in central Alberta. These data were used to evaluate if an estimate of the large zooplankton would improve the TP–Chl model for Alberta lakes.

2. MATERIALS AND METHODS

2.1 THE STUDY LAKES

A preliminary study of eight lakes was made in 1980. These eight lakes plus 19 new lakes were studied in 1981, and 10 of these lakes plus two new lakes were studied in 1982. Data were collected in 1980 and 1981 to evaluate the TP–Chl relationship for local lakes. Data were collected in 1982 to evaluate seasonal fluctuations in TP in local lakes. Data were collected on all lakes in 1980 and 1982 and on 15 lakes in 1981 to study the importance of PP > 250 μm.

The 29 lakes in this study are situated in glacial till and are located in the boreal mixed wood and lower foothills transition biomes in central Alberta. The geographical locations are given in Table 1. Baptiste and Amisk lakes both have two distinct basins joined by a channel. These basins are treated as separate lakes.

2.2 SAMPLE COLLECTION AND ANALYSIS

In 1981, two groups, the limnology group at the University of Alberta and the Water Quality Control Branch of Alberta Environment, participated in this study. Identical sampling methods were employed by both groups. Most of the analyses were performed at the University of Alberta. Where analyses were carried out by both groups, identical techniques were employed. When different techniques were employed, appropriate comparisons are given.

2.3 PHYSICAL DATA ON THE LAKES

Lake surface areas were determined from 1:50 000 topographic maps. Bathymetric surveys were conducted on 13 lakes with a Furuno model FE–400 depth–sounder, and morphometric data were calculated after Hutchinson (1957). Morphometric data for the other lakes were obtained from Alberta Environment and Alberta Energy and Natural Resources.

Table 1. Background data for the 29 study lakes: location, surface area, mean depth (z), and total dissolved solids (TDS), alkalinity (as calcium carbonate), colour, and turbidity in the epilimnion. Chemical values are averages of 1981 and 1982.

Lake	Lat.– (N)	Long.– (W)	Area (km^2)	z (m)	TDS (mg/L)	Alkalinity (mg/L)	Colour (mg/L Pt)	Turbidity (JTU)
Amisk N.	54 35'	112 37'	1.89	10.7#	209	160	15	2.9
Amisk S.	54 35'	112 37'	2.27	19.4#	212	159	14	2.8
Baptiste N.	54 45'	113 33'	4.74	5.9	206	157	17	3.6
Baptiste S.	54 45'	113 33'	4.43	12.7#	208	156	18	2.7
Birch	53 45'	114 32'	7.51	4.5	188*	ND	ND	ND
Bourque	54 40'	110 33'	5.00	8.3	187*	ND	ND	ND
Cooking	53 26'	113 02'	44.3	2.4	1108*	450*	45*	15*
Eden	53 35'	114 09'	0.41	6.2	115	84	6	0.8
Ethel	54 32'	110 21'	4.83	6.6	182*	164*	ND	ND
Halfmoon	53 27'	113 06'	0.57	4.8#	188	128	12	3.4
Hasse	53 29'	114 10'	0.81	3.6#	306	143**	5**	2.0**
Hastings	53 25'	112 55'	9.06	3.7	748*	269*	19*	4.2*
Hilda	54 31'	110 26'	3.62	6.2	480*	ND	ND	ND
Hubbles	53 34'	114 05'	0.45	9.9#	390*	138*	4*	0.5*
Joseph	53 17'	113 04'	6.68	2.4	1545*	910*	55*	34*
Lessard	53 47'	114 39'	3.41	3.8#	166**	132**	2**	5**

continued ...

Table 1. Concluded.

Lake	Lat.– (N)	Long.– (W)	Area km²	z (m)	TDS (mg/L)	Alkalinity (mg/L)	Colour (mg/L Pt)	Turbidity (JTU)
Marie	54 38'	110 18'	36.2	14.1	171*	ND	ND	ND
Mink	53 31'	114 14'	0.70	4.6#	1160	138	4	1.5
Moore	54 31'	110 31'	9.30	8.3	476*	376*	5*	1.9*
Nakamun	53 53'	114 12'	3.16	4.4#	190	137	18	11.5
Narrow	54 35'	113 37'	3.33	14.2#	190*	157*	8*	1.0*
Peanut	54 01'	114 21'	0.30	6.1#	352**	308**	8**	1.0**
Roi	53 35'	114 05'	0.06	8.2	412*	222*	5*	1.0*
Sauer	53 35'	114 05'	0.23	4.2	138	90	6	1.2
Star	53 31'	114 15'	0.27	3.9	694*	80*	30*	0.1*
Tucker	54 32'	110 37'	7.22	2.9	249*	203*	10*	6.5*
Twin	52 55'	114 20'	0.24	15.8#	198	178	18	0.5
Wizard	53 07'	113 55'	2.18	6.2#	202	173	13	2.5
Wolf	54 42'	110 57'	30.6	9.5	210*	ND	ND	ND

– Gazetteer of Canada, Vol. 6 1965.

Calculated from morphometric data collected from 1980 to 1982, University of Alberta.

* 1981 data only.

** 1982 data only.

2.4 SAMPLING REGIME

The lakes were sampled from four to seven times from early May until the end of August 1980, from three to five times from early May until mid-August in 1981, and from six to eight times from mid-May until the end of September in 1982. Each year, sampling began within two weeks of ice melt. Vertical profiles of temperature and light at the deepest site were measured on each visit. Temperature was measured at 1-m intervals with a resistance thermometer accurate to 0.1° C; epilimnetic, metalimnetic, and hypolimnetic zones of the water column were defined according to Hutchinson (1957). The depth of the euphotic zone was defined as twice the Secchi disk reading in 1980, and as 1% surface penetrating irradiance as measured with a Lambda L1-185 light meter with a quantum sensor or a Protomatic photometer in 1981 and 1982.

In the lakes which were deep enough to remain thermally stratified through the summer, water samples were collected with a 1.5-L aluminum drop-sleeve water bottle at the deepest site to determine the vertical distribution of dissolved oxygen, TP < 250 µm, Chl *a* and, in select cases, total dissolved phosphorus (TDP) concentrations. Samples were collected at the same location on each visit.

Dissolved oxygen was determined on water samples collected at 1- to 2-m intervals from the middle of the metalimnion to the bottom of the water column or until dissolved oxygen levels reached zero. Phosphorus profiles were established from samples collected at 1- to 5-m intervals from the surface to within 2 m of the sediment-water interface. Chlorophyll profiles were constructed from samples collected at 1-m intervals from the surface to the bottom of the euphotic zone.

Total phosphorus < 250 µm, Chl *a*, PP > 250 µm, and TN and TDP concentrations were determined from pooled samples collected at 3 to 20 stations in each lake. The number of stations increased proportional to lake surface area and trophic status. Integrated samples for TP < 250 µm, Chl *a*, and TN were collected from the epilimnetic and euphotic zones at each station with weighted Tygon tubing. Similarly, samples for TDP were collected from the epilimnion. At no time was the Tygon tubing allowed to go deeper than 2 m above the bottom. In order to avoid changes in the water samples during storage, all containers were completely filled.

Particulate phosphorus > 250 µm was sampled with a conical net 90 cm long with a 29-cm diameter aperture and fitted with a modified Birge-Juday bucket made with 250-µm Nitex mesh. This fraction was collected from the euphotic zone in all lakes in 1981 and 1982. In deeper lakes, samples were collected to three or four depths in 1980 and 1981. The samples were rinsed with double-distilled water (DDW) (in 1980 and 1981) or lake water (1982) into 175-mL Nalgene bottles; hauls taken to the same depth from all stations on the lake were pooled. Duplicate sets of samples were collected for each lake on each sampling date in 1982.

A 40-L Schindler-Patalas Plexiglas trap fitted with a 250-µm Nitex mesh funnel and bucket was used to estimate the efficiency of the 250-µm tow net. Trap samples were taken at 0.5-m intervals in the euphotic zone. Duplicate tow net samples were taken before and after each set of trap samples to allow for migration of particles up or down in the water column while the trap samples were being collected. Net efficiency was calculated by assuming the Schlinder-Patalas trap was 100% efficient and comparing the amount of phosphorus collected by the trap with the amount of phosphorus collected by the tow net over the same depths. The amount of phosphorus was corrected for the different volumes of water filtered by the two devices (Prepas and Rigler 1982).

The large particles were sampled with a 250-µm net as Prepas and Rigler (1982) had done. Prepas and Rigler found no difference between PP collected with 80 and 250 µm tow nets fitted with a 250 µm bucket. These results were puzzling; they suggested that PP between 80 and 250 µm was very insignificant. To evaluate the importance of PP > 80 µm as compared with PP > 250 µm, two separate tests were performed: (1) seven duplicate profiles were collected from four lakes with a Schindler-Patalas trap fitted with a 250-µm and an 80-µm Nitex net; and (2) duplicate sets of tows were taken in the euphotic zone of nine lakes with tow nets and buckets made with 250-µm and 80-µm Nitex mesh.

2.5 SAMPLE ANALYSES

Dissolved oxygen was determined on water samples which were fixed in the field, chilled, and analysed within 24 h by Carpenter's (1965) modified Winkler technique.

Total nitrogen was calculated as the sum of total Kjeldahl nitrogen (TKN), nitrite–N (NO_2) and nitrate–N (NO_3). Inorganic nitrogen was calculated as the sum of ammonia–N (NH_4), NO_2, and NO_3. Total Kjeldahl nitrogen was determined on samples which had been placed in 250-mL polystyrene containers and preserved with 0.25 mL of concentrated sulphuric acid. These samples were pre–filtered through a 250–µm Nitex net (after Dillon and Rigler) and digested by the sulphuric acid–copper sulphate method of D'Elia et al. (1977) with the following modifications: Hengar granules (obtained from Fisher Scientific Company, Edmonton) were used instead of glass beads, the digested samples were neutralized with a 50% solution and a 0.5% solution of NaOH, and, if the pH went above 6.0, a solution of 10% sulphuric acid was added to lower it to 5.2. These samples were analysed by Solorzano's (1969) phenolhypochlorite method. Ammonia was determined on samples which were stored in 250–mL polystyrene containers and analysed by the method of Solorzano. Nitrate–nitrite was determined on samples which had been collected in 1–L Nalgene polyethylene bottles, filtered through pre–washed 0.45–um HAWP Millipore membrane filters, and analysed by the cadmium–copper reduction method of Stainton et al. (1977). All samples were stored at 5° C from the time of collection and analysed within 24 h for NH_4, and within 48 h for NO_2, NO_3, and TKN. The containers used to store water for nitrogen analyses were cleaned with DDW.

Total phosphorus < 250 µm was determined on samples which had been collected in 1–L acid–washed Nalgene bottles and, within 4 h of collection, pre–filtered through a 250–µm Nitex net and transferred to culture tubes. They were digested and analysed by Menzel and Corwin's (1965) potassium persulphate method as modified by Prepas and Rigler (1982). Particulate phosphorus > 250 µm and PP > 80 µm were determined on samples which were diluted, subsampled, homogenized, subsampled, and digested with potassium persulphate as outlined in Prepas and Rigler (1982). In all but the last section of this study (Section 7), TP refers

to TP < 250 µm (after Dillon and Rigler 1974a). In Section 7, PP > 250 µm was also included and TP was calculated as the sum of TP < 250 µm and PP > 250 µm. Glass culture tubes and Kjeldahl flasks used in nitrogen and phosphorus analyses were rinsed three times with DDW after use. All other glassware was washed in 2% HCl acid, then rinsed four times with distilled water and three times with DDW. All nitrogen and phosphorus determinations were done in triplicate.

To determine the contribution of zooplankton to the large particulate fraction, the zooplankton > 250 µm were separated from PP > 250 µm and analysed for TP. The samples, collected for PP > 250 µm, were made up to a known volume (between 100 and 250 mL) with DDW. Three 10-mL sub-samples were placed in a 175-mL Nalgene bottle and analysed for PP > 250 µm as described previously. The remainder of the sample was rinsed into a graduated cylinder with DDW and made up to a recorded volume (between 100 and 250 mL). To separate the zooplankton from other particles (i.e., phytoplankton) > 250 µm, carbon dioxide gas was gently bubbled through the sample. In 2 to 10 min the narcotized zooplankton settled to the bottom of the cylinder while the plants remained suspended in the water column. Phosphorus in phytoplankton > 250 µm was determined from three 10-mL subsamples taken from the graduated cylinder and placed in a Nalgene bottle. The remaining water lying over the narcotized animals was then carefully siphoned off, leaving the animals concentrated in a small volume of water. The sample was made up to a recorded volume (50 to 100 mL) with DDW and three 10-mL subsamples were placed in a Nalgene bottle. These subsamples were designated the animal portion of the large particulate fraction (ZP > 250 µm) and analysed for TP following the same procedure used for PP > 250 µm. Duplicate samples were collected in 1982 for determination of PP > 250 µm and ZP > 250 µm. The repeatability of the collection and analytical techniques was reasonable; the average standard error of the mean was 10% of the mean concentration for both PP > 250 µm and ZP > 250 µm. The values reported for PP > 250 µm and ZP > 250 µm are the averages of the duplicate samples. When there were large differences (> 50%) between the duplicate samples, the phosphorus in the plant fraction was also analysed as a check on the recorded values.

Two techniques were used to determine [Chl *a*] in 1981. In both cases,

water samples were collected in opaque 1- to 2-L Nalgene bottles. Duplicate sub-samples were prepared within 4 h of collection by filtering 50 to 500 mL of lake water, depending on cell density, through glass fibre filters. The laboratory at the University of Alberta subsequently employed a spectrophotometric technique based upon the ethanol extraction procedure of Ostrofsky (unpublished) described by Bergmann and Peters (1980). Sample filters, which had been rinsed with 1 mL of a saturated $MgCO_3$ solution, were placed in sealed petri dishes, protected from light with aluminum foil, and frozen. Analysis was completed within two weeks of collection. The laboratory at Alberta Environment employed the fluorometric procedure using the acetone extraction of method of Yentsch and Menzel (1963) as modified by Holm-Hansen et al. (1965). Sample filters were placed directly in acetone and refrigerated in the dark; analyses were completed within one week. All samples collected in 1980 and 1982 were analysed by the ethanol extraction technique.

Although differences between the fluorometric and spectrophotometric techniques have been reported (Cullen 1982), no evidence of significant disagreement between the two techniques was found, even though only the fluorometric procedure employed a phaeophytin correction. The fluorometric technique was used for samples collected from 10 lakes in this study. To compare the two methods, 29 duplicate sets of samples were collected from these 10 lakes and analysed by both techniques. The results, which ranged from 3 to 68 mg/m^3 Chl *a*, were highly correlated ($r^2 = 0.99$, $P < 0.0001$) and there was no evidence that one method gave results which were consistently higher or lower than the other method (paired *t*-test, $P > 0.5$).

Total dissolved solids, alkalinity, colour, and turbidity were determined during the summer of 1981 and 1982 on epilimnetic water samples which were collected in 1-L acid-washed Nalgene bottles. Samples were stored at 5° C from time of collection and were analysed within 48 h. Total dissolved solids was determined on 50 mL of water if conductivity was greater than 500 µmho/cm, or on 100 mL of water if less than 500 µmho/cm. The samples were filtered through washed 0.45-µm HAWP membrane filters, and placed in a pre-weighed porcelain evaporating dish. They were then evaporated at 105° C for 16 h, cooled in a desiccator, and re-weighed. Total dissolved solids were calculated as outlined in Stainton et al. (1977). Alkalinity

was determined by the potentiometric titration method of Environment Canada (1979). Colour was measured visually, after samples were centrifuged for 10 min, on a Hazen Platinum–Cobalt scale with Hellige Aqua Tester Model 611A. Turbidity was measured using a Hach Turbidimeter Model 2100A.

All regressions were performed on the Amdahl model 580/2 computer at the University of Alberta. Statistical analyses are as outlined in Snedecor and Cochran (1980). Range rather than variance is used as an estimate of dispersion in cases where the sample size is small and the distribution unknown.

Some data collected in 1978 on Bob Lake (Haliburton region, Ontario) are also included in this report. The methods of collection and analyses were identical to those outlined here. Background information on Bob Lake is in Prepas and Rigler (1982).

3. GENERAL CHARACTERISTICS OF THE STUDY LAKES

The study lakes are fairly representative of small and medium-sized lakes in central Alberta. They are located over a large region (7×10^4 km^2) in central Alberta, in the drainage basins of three major river systems (Athabasca, Beaver, and North Saskatchewan rivers). The total dissolved solids range from 128 to 1545 mg/L, and on this basis the lakes can be classified as either freshwater (TDS < 500 mg/L) or saline (TDS > 500 mg/L) (Rawson 1951). The lakes are not heavily coloured (2 to 55 mg/L platinum), are alkaline (80 to 910 mg/L $CaCO_3$), and most are not very turbid (0.1 to 34 Jackson Turbidity Units [JTU]). The study lakes encompass a wide range of sizes (surface areas 0.06 to 36 km^2), depths (mean depths 2.4 to 19 m), and mixing patterns (Tables 1 and 2). In summer, the surface water inflow to most small and medium-sized lakes in central Alberta is minimal due to low rainfall and small catchment areas. Thus, changes in TP levels in the surface waters in summer are controlled by internal rather than external factors. During the open water season, 11 lakes mixed intermittently (although one of these, Hasse, does not fall clearly into either category) and 16 were permanently thermally stratified. However, profiles of total dissolved solids, temperature, and dissolved oxygen revealed that 14 of the 16 stratified lakes were partially meromictic and another lake, Roi Lake, was permanently meromictic.

The stratified lakes had low or non-detectable dissolved oxygen levels and correspondingly high TP values in the hypolimnia during summer, and deep chlorophyll peaks were observed in the less productive lakes. Deep chlorophyll maxima were observed in six lakes in 1981 (Eden, Hubbles, Narrow, Roi, Sauer, and Twin). In these lakes, an average of 80% of the euphotic zone chlorophyll (m^{-2}) was found below the epilimnion. These deep chlorophyll maxima may develop in response to high nutrient and adequate light levels (Fee 1976). It is also possible that some of this deep chlorophyll is phaeophytin; however, this parameter was not estimated in these lakes.

Table 2. Nutrient and chlorophyll data and the thermal characteristics for the 27 lakes studied in 1980 and 1981: summer thermal regime (S, stratified; M, isothermal), spring total phosphorus (TP), mean summer chlorophyll *a* (Chl *a*), mean summer euphotic TP, mean summer epilimnetic TP, mean epilimnetic TP:spring TP ratio, total nitrogen (TN):TP ratio in spring, and TN:TP ratio for the euphotic zone in summer. Data for these lakes studied in 1980 and 1981 are presented in chronological order.

Lake		Spring TP (mg/m³)	Summer Chl *a* (mg/m³)	Summer Euphotic TP (mg/m³)	Summer Epilimnetic TP (mg/m³)	Summer Epilimnetic TP Spring	Spring TN:TP	Summer Euphotic TN:TP
Amisk N.	S	66.0	21.6	37.9	36.8	0.56	ND	ND
		ND	18.3	31.6	31.7	ND	ND	54
Amisk S.	S	68.7	21.0	38.6	37.4	0.54	ND	ND
		ND	20.7	33.0	32.0	ND	ND	40
Baptiste N.	M	57.8	34.1	65.6	ND	1.13*	ND	ND
		ND	34.8	46.2	44.5	ND	ND	31
Baptiste S.	S	79.9	50.9	55.3	48.8	0.61	ND	ND
		ND	26.0	38.0	34.4	ND	ND	37
Birch	M	45.2	21.7	53.8	ND	1.19*	33	25
Bourque	S	16.4	4.8	19.1	17.1	1.04	49	37
Cooking	M	303	158	274	ND	0.90*	14	29
Eden	S	28.7	9.2	19.6	16.2	0.56	37	36
Ethel	S	34.6	6.3	19.9	19.0	0.55	22	44
Halfmoon	M	ND	46.2	95.8	ND	ND	ND	29
Hasse	M	27.0	3.3	21.4	21.4	0.79	53	54
Hastings	M	152.0	80.6	156	158	1.03*	13	27
Hilda	S	28.3	5.6	25.7	22.2	0.78	43	44
Hubbles	S	27.1	10.4	ND	15.8	ND	ND	ND
		26.2	7.6	20.7	20.3	0.77	39	50
Joseph	M	761	89.0	755	ND	0.99*	5	9
Marie	S	15.8	5.5	16.0	13.8	0.87	49	40
Mink	M	24.7	5.3	26.9	26.6	1.09*	49	39
Moore	S	33.9	4.7	23.6	22.4	0.66	29	48
Nakamun	M	53.1	41.7	155	150	2.92*	ND	ND
		78.4	150	155	124	1.98*	18	20

continued ...

Table 2. Concluded.

Lake	TP	Spring Chl *a* (mg/m³)	Summer Euphotic (mg/m³)	Summer Euphotic TP (mg/m³)	Summer Epilimnetic TP (mg/m³)	Summer Epilimnetic TP Spring	Spring TN:TP	Summer Euphotic TN:TP
Narrow	S	ND	2.2	12.5	12.2	ND	ND	ND
		11.1	3.4	11.8	10.1	0.91	51	45
Roi	S	13.4	5.8	14.8	9.8	0.73	62	64
Sauer	S	33.0	18.6	31.7	18.3	0.55	39	38
Star	S	28.8	5.4	21.2	20.8	0.72	40	50
Tucker	M	29.1	30.0	58.9	53.4	2.02*	32	18
Twin	S	21.4	1.7	12.0	11.7	0.55	ND	ND
		16.3	2.3	12.8	9.6	0.59	22	26
Wizard	M	36.3	26.4	44.2	45.6	1.22*	26	25
Wolf	S	39.4	7.3	21.3	19.7	0.50	24	41

* Summer TP in the euphotic zone used in the ratio.

4. PHOSPHORUS-CHLOROPHYLL MODELS

4.1 THE INPUTS TO THE PHOSPHORUS-CHLOROPHYLL MODEL

Since we were planning to compare the TP-Chl relationship in the eight lakes studied in 1980 and the 27 studied in 1981 with Dillon and Rigler's (1974) model, we attempted to keep our methods and periods of collection as similar to theirs as possible. Dillon and Rigler's model has two variables, spring [TP] and mean summer [Chl*a*] in the euphotic zone. They assumed that: (1) [TP] was homogenous throughout the water column at spring overturn; (2) there was a clear division between spring overturn and summer stratification; and (3) in summer all water in the euphotic zone was suitable for algal production. However, these assumptions did not hold for the lakes in this study.

Variables in the TP-Chl model were therefore modified in three ways to accommodate the conditions in the study lakes:

1. Since there was no method to determine whether phosphorus in anoxic water was available for the production of summer algal biomass, spring [TP] was calculated only from water collected in the portion of the water column which had detectable levels of dissolved oxygen.
2. The transition from spring to summer is usually defined as the onset of permanent thermal stratification. This general definition was not used because 10 lakes in the study did not stratify permanently during the summer period and 14 more were stratified from ice-out. Spring was thus arbitrarily defined for 1980 and 1981 as the period from ice-out until the end of the third week in May and summer from the beginning of the fourth week in May until the end of August.
3. Since algal production is usually limited to water with detectable levels of dissoved oxygen, the portion of the euphotic zone containing anoxic water was excluded from the integrated summer samples.

4.2 PHOSPHORUS–CHLOROPHYLL RELATIONSHIPS IN ALBERTA LAKES

The relationship between spring [TP] and mean summer [Chl *a*] derived for the lakes in this study was similar to that predicted by Dillon and Rigler's model. The data are evenly scattered above and below Dillon and Rigler's regression line ($\chi^2 = 0.14$, $P > 0.5$) (Figure 1). We thus found no evidence that lakes in western Canada produce consistently less chlorophyll per unit phosphorus than other temperate lakes. The TP–Chl relationship in our lakes (Table 2) was:

$$\log [\text{Chl } a] = -0.676 + 1.119 \log [\text{TP}]\text{sp} \qquad (1)$$

($n = 29$, $r^2 = 0.67$), where [TP]sp is spring [TP]. There were two differences between this relationship and Dillon and Rigler's model:

$$\log [\text{Chl } a] = -1.136 + 1.448 \log [\text{TP}]\text{sp} \qquad (2)$$

($n = 46$, $r^2 = 0.90$). Equation 1 accounts for significantly less variation than Equation 2 (two–tailed F–test, $P < 0.05$). Secondly, the slope in Equation 1 is much lower than in Equation 2, although this difference could not be tested statistically due to variance heterogeneity. These differences, which will be discussed in detail below, appear to be a function of the properties of Alberta lakes.

One factor which could explain the high variance of the data used for Equation 1 is the variability in the relationship between spring and summer [TP] in these lakes. It is often assumed that there are only small seasonal changes in within–lake [TP] (Dillon and Rigler 1974), with spring [TP] being slightly higher than either mean summer (Nicholls and Dillon 1978) or mean annual [TP] (Chapra and Tarapchak 1976). The mean summer [TP]: spring [TP] ratio in 12 lakes studied by Dillon and Rigler was 0.87, and this relationship was quite consistent ($r^2 = 0.92$, Nicholls and Dillon 1978). However, the summer [TP]: spring [TP] ratio in this study was not at all consistent, varying from 0.5 to 3 (Table 2).

Although our lakes form a continuum with respect to the summer TP:spring TP ratio, they can be roughly divided into three groups: (1)the shallow productive freshwater lakes (i.e., do not permanently stratify in summer, have mean summer [Chl *a*]

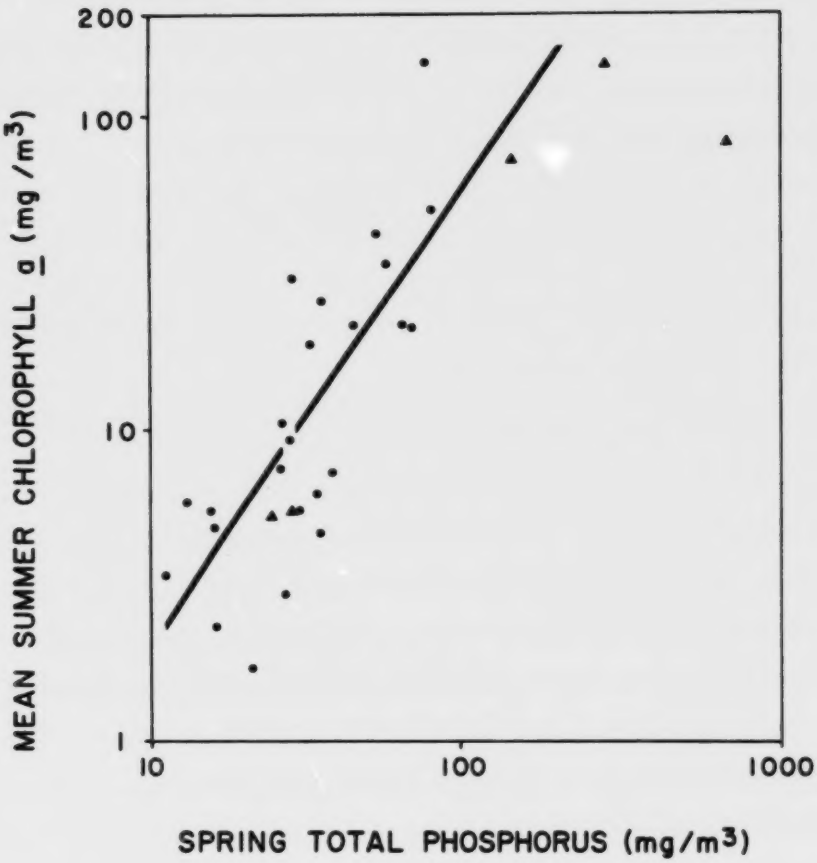

Figure 1. Relationship between mean summer chlorophyll and total phosphorus at spring overturn in lakes in central Alberta. Triangles (▲) indicate saline lakes. The line is from Dillon and Rigler (1974).

which is greater than 10 mg/m³, and have less than 500 mg/L total dissolved solids); (2) the shallow saline lakes (i.e., do not permanently stratify in summer and have more than 500 mg/L total dissolved solids); and (3) the other lakes (most of which had permanent thermal stratification in summer).

The summer [TP] in the shallow productive freshwater lakes (i.e., Baptiste N., Birch, Nakamun, Tucker, and Wizard) was higher than spring [TP] and fluctuated dramatically, as illustrated in Figure 2 with data from Nakamun Lake. In this group, the average summer TP:spring TP ratio was 1.74 (range 1.2 to 2.9; Table 2). However, in the shallow saline lakes (i.e., Cooking, Hastings, Joseph, and Mink) the [TP] remained fairly stable throughout the study period and there was apparently no significant change in [TP] between spring and summer. The average summer TP:spring TP ratio for these lakes was 1.00 (range 0.9 to 1.1; Table 2). However, most of the stratified lakes had mean summer TP levels which were lower than spring values, although the changes in [TP] in these lakes were fairly gradual, as illustrated in Figure 2 with data from Twin Lake. The average summer TP:spring TP ratio for these lakes (n = 18) was 0.68 (range 0.50 to 1.04; Table 2). Thus three quite distinct patterns of seasonal TP levels were observed.

The seasonal fluctuations in the euphotic zone [Chl *a*] paralleled those of [TP] in most cases. This was shown by fitting regression lines to paired measurements of summer TP and chlorophyll levels in the euphotic zone of each lake which had three or more pairs of points per summer. Because the number of points used to construct each regression line was too small (i.e., three to seven) to test the significance of the individual lines, the probabilities were combined following a technique outlined in Sokal and Rohlf (1981, Box 18.1). Total phosphorus and chlorophyll levels were correlated during summer on a day–to–day basis within lakes (χ^2– test, $P < 0.025$).

This correlation between paired measurements of [TP] and [Chl *a*] in individual lakes implies that summer [TP] rather than spring [TP] should be the best predictor of summer chlorophyll when there is substantial variation in the seasonal patterns of [TP]. The summer TP–Chl relationship (Table 2) was:

$$\log [\text{Chl } a] = -0.661 + 1.146 \log [\text{TP}]_{su} \qquad (3)$$

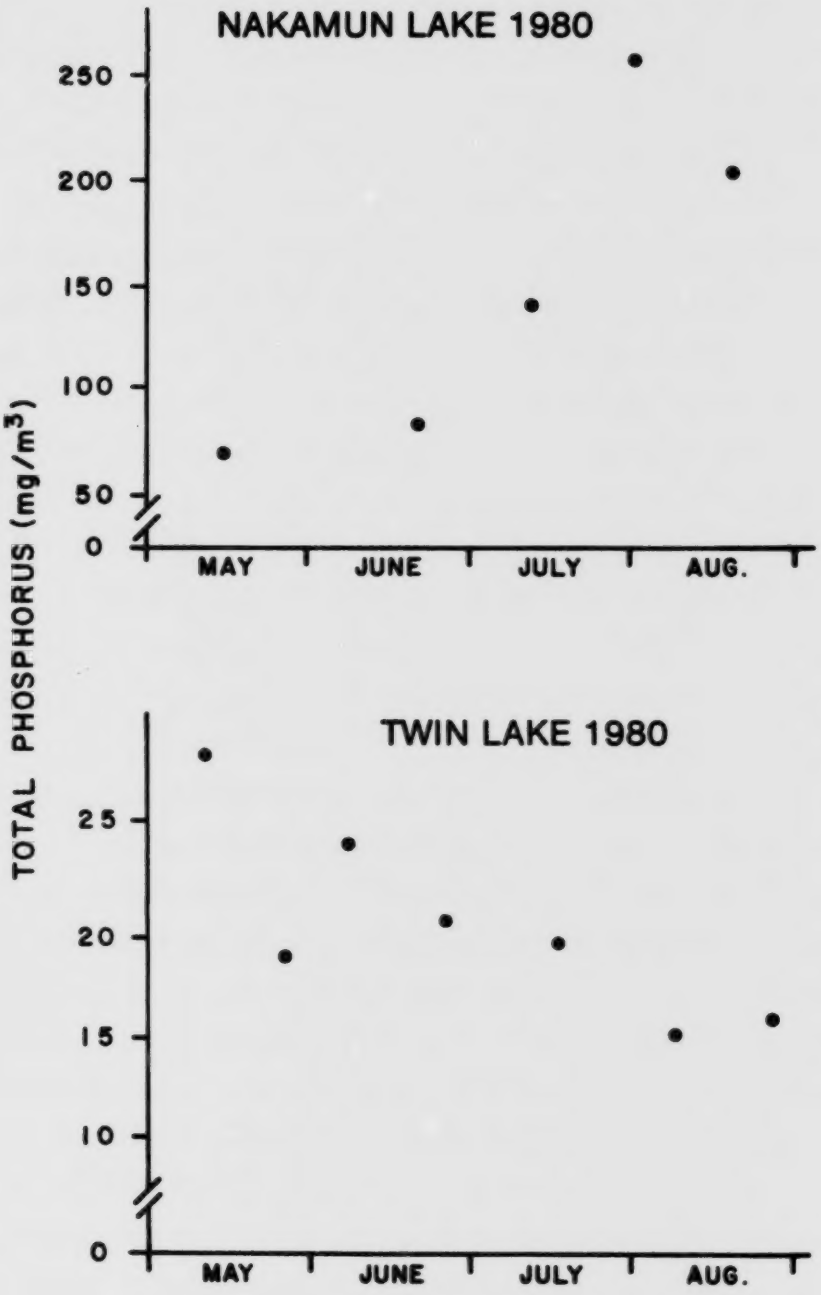

Figure 2. Total phosphorus concentration in the euphotic zone of a shallow lake, Nakamun, and a deep lake, Twin, from May until August 1980.

(n = 34, r^2 = 0.81) where [TP]su is mean summer [TP] in the euphotic zone. Although the slope of Equation 3 is similar to Equation 1, the variation around Equation 3 is much less than for Equation 1 and is not different from Dillon and Rigler's model (two-tailed F-test, $P > 0.5$).

A portion of the variance in Equation 1 could also be caused by poor chlorophyll estimates for the productive lakes. Spatial and temporal fluctuations in chlorophyll were greatest in these lakes. The sampling program was not, however, adjusted to accommodate all of these fluctuations because sufficient baseline data were not available. An intensive study of the chlorophyll fluctuations in productive lakes is required to design better sampling programs for these lakes and to evaluate the data presented here. The lower slope in Equation 1 as compared to Equation 2 could be caused by the presence of saline lakes. In this study there were five saline lakes (Cooking, Hastings, Joseph, Mink, and Star), all with relatively low Chl:TP ratios (Figure 1), whereas there were no saline lakes in Dillon and Rigler's study. Additionally, Joseph Lake, which showed the greatest deviation from Equation 1, was the most saline. When the saline lakes were removed, the TP-Chl relationship was

$$\log [\text{Chl } a] = -1.327 + 1.573 \log [\text{TP}]\text{sp} \qquad (4)$$

(n = 24, r^2 = 0.63). The slope of Equation 4 is higher than our original equation (Equation 1), and very similar to Equation 2 (t-test, $P > 0.5$). Although the sample size is very small, the differences between Equations 1 and 4 are evidence that saline lakes have lower Chl:TP ratios than freshwater lakes. More saline lakes should be studied to determine whether this ratio is consistently low.

The three most productive saline lakes, Cooking, Hastings, and Joseph, also had low TN:TP ratios in spring: 13, 14, and 5, respectively. However, the TN:TP ratios in these three lakes doubled during the summer; the corresponding mean summer ratios were 29, 27, and 9 (Table 2). Thus, only the summer TN:TP ratio in Joseph was low, although it is not considered a low ratio by some investigators (e.g., Schindler 1977). Joseph not only had the lowest TN:TP ratio, but also had the highest dissolved solids and turbidity levels (Table 1), and thus was an outlier in several ways. When Joseph was excluded from Equation 1, the slope of the equation increased, but

was still lower than in Dillon and Rigler's model (Equation 2). It is difficult to understand why the Chl:TP ratio is so low in this lake. It could be due to a combination of factors: the low TN:TP ratio, high light extinction caused by high turbidity, and the high level of dissolved solids.

4.3 NITROGEN–CHLOROPHYLL RELATIONSHIP IN ALBERTA LAKES

Total nitrogen and mean summer chlorophyll were highly correlated in this study (Table 2), the r^2 was 0.57 for the spring TN–Chl relationship and 0.74 for the summer TN–Chl relationship. However, these correlations were weaker than for the corresponding TP–Chl relationship (r^2 =0.67 and 0.81 respectively). When TN and TP were used in a multiple regression to predict chlorophyll, TN did not add more information than TP alone (t–tests, P >0.4) since TN and TP were highly correlated (e.g., the r^2 for mean summer values was 0.86). Inorganic nitrogen did not follow the same pattern as TN. There was no significant relationship between either spring or summer inorganic nitrogen in the euphotic zone and mean summer chlorophyll (t–tests, P > 0.25). Thus, as also noted in other studies (Smith 1979), nitrogen has less predictive power for chlorophyll biomass than does TP.

4.4 DISCUSSION OF PHOSPHORUS–CHLOROPHYLL MODEL

Not only was the TP–Chl relationship in our study lakes similar to those reported for lakes on the Precambrian Shield (Dillon and Rigler 1974), but the TN:TP ratios were also similar. The mean TN:TP ratio in spring was 34, and in the euphotic zone in summer it was 37. Both the Chl:TP and the TN:TP ratios are, however, much higher than those reported by Gallup (1978) and Hickman (1980) for lakes in the same area, and in three cases, for the same lakes.

We investigated whether these differences were caused by poor estimates of [TP] in the previous studies. Water samples were analysed for [TP] from seven of the lakes studied by Gallup and Hickman in addition to the three included in this study. In all cases, our [TP] values were lower than Gallup and Hickman's (Table 3). The differences range from two–fold to more than an order of magnitude. These differences are due to the analytical methods used by Gallup and Hickman. Their

Table 3. A comparison of total phosphorus concentrations (TP mg/m³) reported by Gallup (1978) and Hickman (1980) and data collected in this study in 10 Alberta lakes.

Lake	Gallup Mean [TP]	Hickman Spring [TP]	This Study	
			Spring [TP]	Mean Summer [TP]
Buffalo	400	300*	ND	62
Cold	270	170	ND	15
Cooking	1100	455*	303	274
Gull	300	325*	ND	44
Hastings	ND	630	152	156
Joseph	ND	2880	761	755
Miquelon	480	1040	ND	172
Moose	300	230*	ND	32
Pigeon	280	165*	ND	32#
Sylvan	320	240	ND	22

* Average for 2 yr.
# Datum provided by H. Hamilton and T. Reynoldson (Alberta Environment).

standards were prepared as phosphate rather than phosphorus standards (i.e., for a standard solution of 10^3 mg P/m^3 they used 0.143 rather than 0.439 g KH_2PO_4 dissolved in 1 L of DDW [G. Hutchinson, Dept. of Zoology, University of Alberta, personal communication]). Total phosphorus concentrations calculated from their standards are thus overestimated by a factor of three. In addition, containers and glassware used for analyses of Gallup and Hickman's samples were washed with Alconox, a detergent containing several parts per hundred phosphorus (G. Hutchinson, personal communication). This detergent caused a high degree of contamination in Gallup and Hickman's samples and explains why the differences between their data and ours were not simply three-fold.

We cannot explain why the TN:TP and Chl:TP ratios reported for the Qu'Appelle Valley lakes in southern Saskatchewan (Allan and Kenny 1978) were so similar to Gallup and Hickman's. However, the Qu'Appelle Valley lakes are saline; total dissolved solids ranged from 887 to 1285 mg/L (Rawson and Moore 1944). If saline lakes generally produce less chlorophyll than freshwater lakes, these lakes would be expected to have low Chl:TP ratios.

The close correlation between levels of TP and Chl *a* and the high TN:TP ratios found in this study suggest that phosphorus is the nutrient controlling the level of phytoplankton productivity in Alberta lakes. This study also suggests that dividing the lakes into three categories (shallow productive, thermally stratified, and saline) would improve the correlation between spring [TP] and summer [Chl]. However, much more information needs to be collected on these lakes before comprehensive eutrophication control schemes can be developed. The seasonal fluctuations of [TP] in the shallow productive lakes and the drop in TP levels during the summer in the thermally stratified lakes were studied in 1982 (Section 6). When and to what extent high levels of total dissolved solids are associated with low phytoplankton biomass is currently being studied at the University of Alberta.

5. TOTAL DISSOLVED SOLIDS AS A PREDICTOR OF LAKE BIOMASS AND PRODUCTIVITY IN ALBERTA LAKES

Total dissolved solids (TDS) was identified as an indicator of benthic, planktonic, and fish biomass and fish production by Rawson (1951, 1960). Later the ratio of TDS to mean depth (z), the morphoedaphic index (MEI), was developed to predict fish production (Ryder 1965). The criteria for use of the MEI for a group of lakes (i.e., where both TDS and z are important parameters) are that the lakes should be subject to a relatively homogeneous set of environmental conditions, with the exceptions that z and TDS should vary over a wide range (Ryder et al. 1974) or that the lakes are part of a sizeable region (Ryder 1982). The MEI has been widely used for lake management, although more recent investigations have shown that chlorophyll concentration (Oglesby 1977), benthic biomass (Matuszek 1978), and concentration of total phosphorus (Hanson and Leggett 1982) were better predictors of fish production than either TDS or the MEI.

Hanson and Leggett have suggested that TDS should be correlated with total phosphorus (TP) because phytoplankton biomass and production in lakes are dependent upon the concentration of TP (Schindler 1977). Since TP and Chl *a* are highly correlated in lakes (Nicholls and Dillon 1978), Chl *a* should also be correlated with TDS. I examined this hypothesis with the data in Tables 1 and 2 for the 27 lakes. These lakes satisfy both of Ryder's conditions under which TDS should be an important parameter. However, there was no relationship between TDS and Chl *a* in these lakes (Figure 3). There was also no relationship between mean summer epilimnetic TDS and TP ($n = 31$, $r^2 = 0.00$, $P = 0.77$ on a log–log scale), whereas TP and Chl *a* were highly correlated (Section 4). Thus TDS was not a good predictor of phytoplankton biomass, as measured by Chl *a*, in these lakes.

None of the 27 lakes were located on the Precambrian Shield, whereas both on–shield and off–shield lakes were included in the previous studies which showed a positive correlation between TDS and productivity (Table 4). The lakes in each of the previous studies are therefore divided into two groups (on–shield and off–shield) in order to determine whether TDS was correlated with productivity within each group. The division between on–shield and off–shield lakes was set at

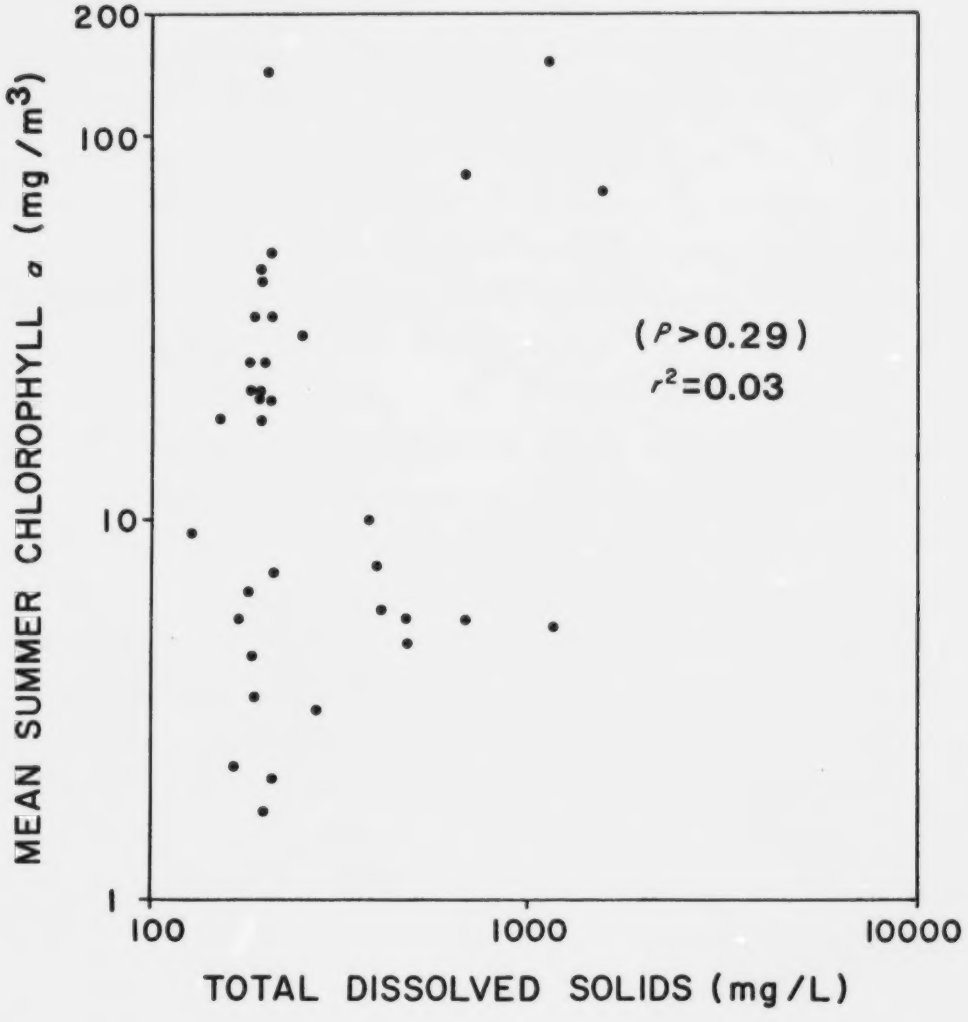

Figure 3. Relationship between summer chlorophyll *a* within the euphotic zone and total dissolved solids within the epilimnion in 27 lakes in central Alberta in 1980 and 1981. There are 35 points because eight lakes were studied in both 1980 and 1981.

Table 4. Relationships between total dissolved solids (TDS) and indices of productivity from reports which include lakes both on and off the Precambrian Shield. All correlations are log–log. Negative correlations are indicated by –, significant correlations by * ($P < 0.05$) or ** ($P < 0.01$).

Variables		Lakes								
		All Areas			On–Shield			Off–Shield		
Source	TDS vs.	n	r^2	P	n	r^2	P	n	r^2	P
Rawson 1961	fish production	12	0.50	**0.01	6	0.23	0.33	6	0.03	0.73
	fish catch	13	0.21	0.12	6	0.79–	*0.02	7	0.03–	0.98
	plankton biomass	13	0.23	0.10	6	0.43	0.16	7	0.03	0.73
	benthic biomass	13	0.59	**0.00	6	0.31	0.25	7	0.00	0.94
Ryder 1965	fish production	23	0.12	0.11	9	0.00–	0.90	14	0.24	0.08
Matuszek 1978	fish production	22	0.19	*0.04	10	0.15	0.27	12	0.03	0.58
	benthic biomass	11	0.43	*0.03	5	0.54	0.16	6	0.15	0.45
	plankton biomass	11	0.49	*0.02	5	0.39	0.26	6	0.20	0.37
Hanson and Leggett 1982+	fish production	40	0.14	*0.02	24	0.00–	0.76	16	0.11	0.20
	benthic biomass	26	0.54	*0.00	12	0.07	0.40	14	0.02	0.63

+ Three lakes, Ijssel and Upper and Lower Constance, were excluded from the analysis because of uncertainty associated with the TDS–yield values. For Ijssel, TDS was reported as chloride (Willemson 1977) and ranged in other reports from 200 to 300 mg/L (J.M. Hanson, personal communication). Hanson and Leggett used a mean value of 250 mg TDS/L, which made Ijssel an outlier, 30% higher than any other lake in the set. When Lake Constance underwent eutrophication, fish yield increased threefold, whereas TDS remained constant (Hartmann and Numann 1977). Hanson and Leggett used only post–eutrophication yield data which were not unique with respect to TDS. When these three lakes are excluded there is no significant log–log relationship betweeen TDS and total phosphorus ($n = 18$, $r^2 = 0.06$, $P = 0.31$).

100 mg TDS/L (Rawson 1951). Lake location was not used to classify lakes because a lake can be located in a different region than its major source of water. Both on-and off-shield lakes cover a large region (e.g., the lakes used by Ryder [1965] and Matuszek [1978] extend from the Northwest Territories north of Alberta to Ontario and from Alberta to Ontario for the two regions, respectively, and the lakes analysed by Hanson and Leggett [1982] include the same territory plus the northern United States and northern Europe). Even though the range of TDS is reduced when a data set is divided into on-shield and off-shield classificatons, these groupings still cover a broad enough range of nutrient concentrations that TDS should be a useful parameter for predicting lake productivity (Ryder et al. 1974; Ryder 1982). However, there was no significant positive relationship between TDS and fish production, TDS and fish catch, TDS and plankton biomass, or TDS and benthic biomass in either on-shield or off-shield lakes. Moreover, in nine cases the correlation coefficients approached zero and there was only one significant negative correlation (Table 4).

Therefore, the previously observed positive correlations between TDS and these indices were only indicators of the differences between on-shield and off-shield lakes. These results suggest that TDS may not be a useful predictor of lake biomass and productivity for Alberta lakes.

6. SEASONAL DYNAMICS OF TOTAL PHOSPHORUS IN ALBERTA LAKES

6.1 THE LAKES USED IN THIS STUDY

The 12 lakes used in this study were: Amisk North, Amisk South, Baptiste North, Baptiste South, Eden, Hasse, Lessard, Mink, Peanut, Sauer, Twin, and Wizard. The location and general characteristics for these are given in Table 1. These lakes were selected to provide variation in size (surface areas 0.2 to 5 km^2), depth (mean depths 3 to 19 m), mixing patterns, and trophic status (levels 1 to 4; Dillon and Rigler 1975). These factors have been associated with various patterns in surface water phosphorus concentrations (e.g., Vollenweider 1976; Section 4 this report). All the lakes had low concentrations of dissolved oxygen by the late winter of 1982 (Babin and Prepas, unpublished). Based on the patterns observed during the summer, the lakes were divided into three categories: (1) those which mixed intermittently (i.e., shallow lakes); (2) those which were permanently thermally stratified (i.e., deep lakes) and where the euphotic zone did not extend into the hypolimnion; and (3) deep lakes where the euphotic zone extended into the hypolimnion.

6.2 SHALLOW LAKES

In the shallow lakes, Mink, Lessard, Baptiste N., and Wizard, the [TP] in the epilimnion decreased during spring and fall mixing and increased during the summer (Figure 4). The shallow lakes were all weakly thermally stratified by June and remained so for at least two months. However, temperature profiles show that during the summer there were periods when the entire water column partially mixed (e.g., 6/15 to 7/6 and 7/27 to 8/17 for Mink Lake,Figure 4) and periods when there was little mixing (e.g., 5/31 to 6/15 and 7/6 to 7/27 for Mink Lake, Figure 4). When mixing was minimal, TP values in the epilimnion tended to stablize or decrease, whereas during partial mixing the [TP] increased. By late summer, these lakes were mainly isothermal, and the [TP] in the surface waters decreased in three of the lakes. (Complete temperature and phosphorus data for these lakes are in Tables 19, 23, 24, 28, 31, 35, 36, and 40).

The data collected on the shallow lakes support the following hypothesis.

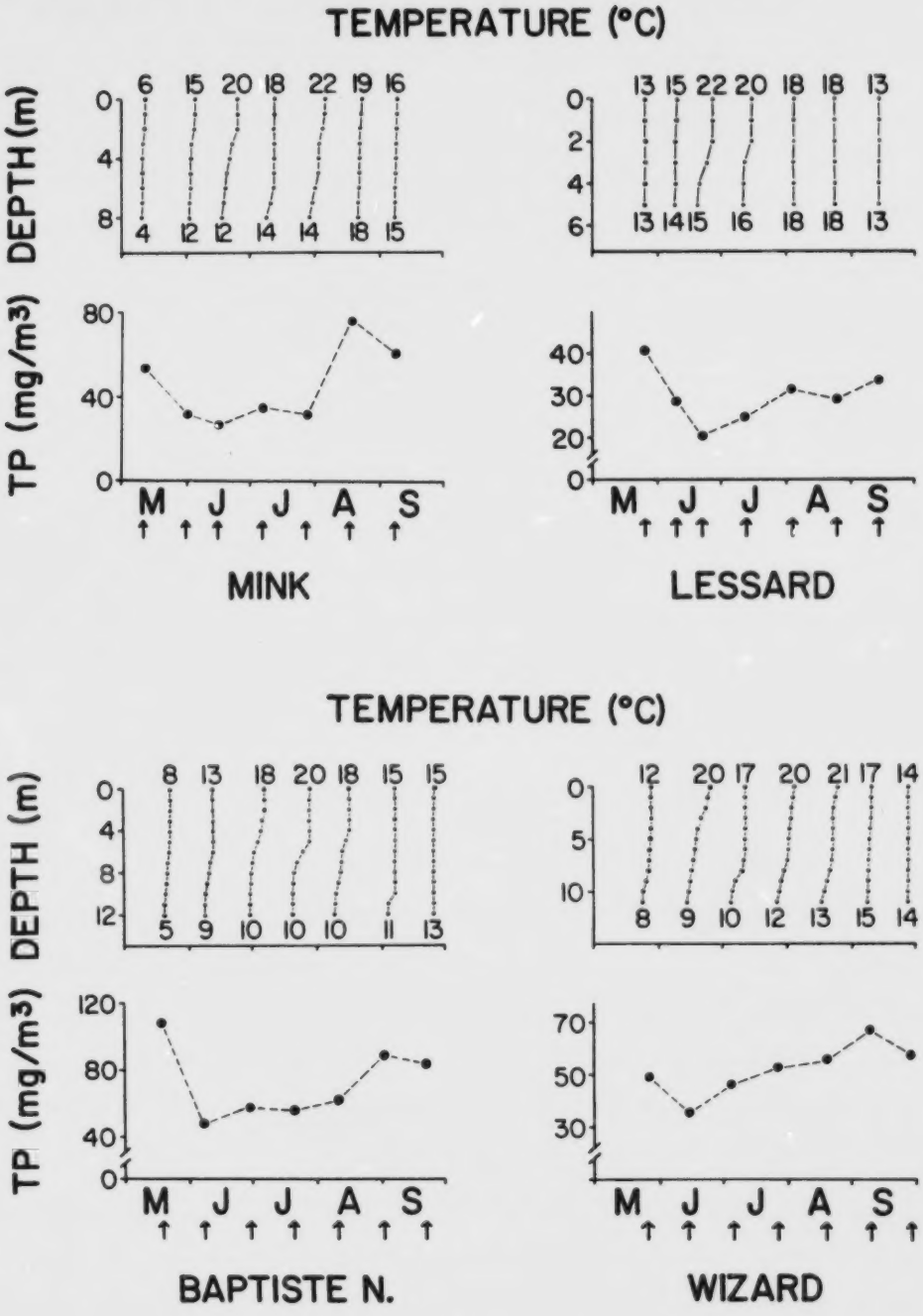

Figure 4. Temporal variation in the vertical distribution of temperature and the concentration of total phosphorus (TP) in the euphotic zone of four shallow lakes in central Alberta in 1982. The average depth of the euphotic zone was 5.5 m, 3.5 m, 4 m, and 4 m for Mink, Lessard, Baptiste N., and Wizard lakes, respectively. Arrows indicate sampling dates.

During the stratified period, TDP rapidly increased in the water overlying the sediments where dissolved oxygen levels were low. There was little exchange between this deep phosphorus pool and the surface waters except when these two strata partially mixed. Mixing occurred intermittently throughout the summer and, thus, the [TP] in the epilimnion increased in spurts. This trend is supported by data on Baptiste N., Lessard, Mink, and Wizard lakes; the change in water temperature at the deepest location sampled was positively correlated with the change in [TP] in the epilimnion during the stratified period in 1982 ($r = 0.75$, $n = 15$, $P < 0.01$). Phosphorus profiles were collected in 1981 on three of these lakes (Mink, Baptiste N., and Wizard). In midsummer 1981, there was a marked increase in the [TP] below the thermocline in these lakes; the difference between the [TP] in deep and surface waters was over an order of magnitude by August.

6.3 DEEP LAKES WHERE THE EUPHOTIC ZONE DID NOT EXTEND INTO THE HYPOLIMNION

Temporal variation in TP in deep lakes where the euphotic zone did not extend into the hypolimnion (i.e., Amisk N., Baptiste S., Amisk S., and Twin), had more predictable patterns than the shallow lakes. Total phosphorus values in the epilimnion decreased sharply in the first three to six weeks after ice-out. Total phosphorus levels remained relatively low during the summer, except in the more productive lakes where it increased in late summer (Figure 5). Dissolved oxygen levels were low in the hypolimnion in spring and decreased systematically throughout the summer partially because these lakes were all meromictic (Figure 5). In the more productive lakes, Amisk N., Baptiste S., and Amisk S., dissolved oxygen levels were < 1 mg/L throughout the hypolimnion by July or August, whereas oxygen depletion occurred much more slowly in Twin Lake which was less productive (Figure 5). Under reducing conditions, TP levels in the hypolimnion increased steadily throughout the summer. There was little apparent transfer from the hypolimnion to the epilimnion for most of the summer. However, there was a noticeable exchange when the thermocline was depressed and there was a large TP gradient at the top of the hypolimnion (i.e., in September in Amisk N., Baptiste S., and Amisk S. [Figure 5]. (Complete temperature and phosphorus

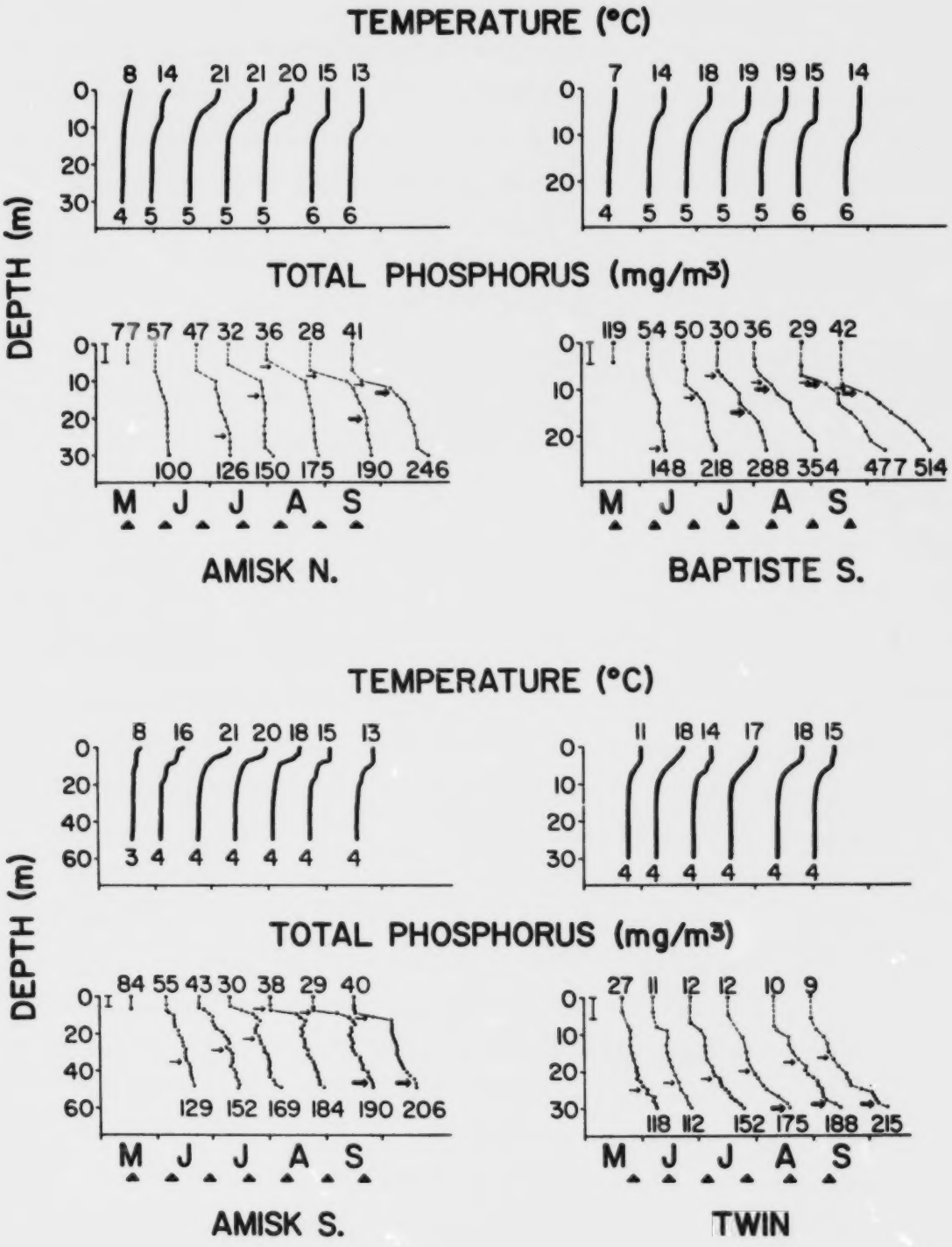

Figure 5. Temporal variation in the vertical distribution of temperature and the concentration of total phosphorus in four deep lakes in central Alberta in 1982. In these lakes, the euphotic zone (indicated by I) did not extend into the hypolimnion. Light arrows (→) and dark arrows (➔) indicate the depths where the dissolved oxygen concentrations were 1 and 0 mg/L, respectively. Triangles (▲) indicate sampling dates.

data for these lakes are in Tables 17, 18, 20, 27, 29, 30, 32, and 39).

The phosphorus in the hypolimnion of these deep lakes was virtually all dissolved (Table 5). Although the TDP to TP ratio varied from 0.33 to 0.63 in the epilimnion of these lakes, it ranged from 0.95 to 0.97 at select depths in the hypolimnion. The volume–weighted rate of increase of TP in the hypolimnion during the summer period was correlated with phytoplankton biomass (Table 6). Mean rates of increase ranged from 14.3 mg/m^2 day^{-1} TP (where m^2 refers to the area of the top of the hypolimnion) in the most productive lake to 3.5 mg/m^2 day^{-1} in the least productive lake. These rates were moderately constant from year to year. Mean rates of increase calculated for three summers (1980 to 1982) ranged from 8 to 10 mg/m^2 day^{-1} TP for Amisk S. and 6 to 8 mg/m^2 day^{-1} for Amisk N.

6.4 DEEP LAKES WHERE THE EUPHOTIC ZONE EXTENDED INTO THE HYPOLIMNION

The lakes Sauer, Eden, and Peanut, were permanently thermally stratified and the euphotic zone extended into the hypolimnion. Total phosphorus values in the epilimnion decreased sharply between spring and summer and remained low through to September in these lakes (Figure 6). Dissolved oxygen levels in the hypolimnion were low throughout the summer, although anoxic conditions were only encountered below the euphotic zone (Figure 6). A local TP maximum developed at the bottom of the euphotic zone of Sauer Lake (Figure 6). The phosphorus buildup in the hypolimnion of these lakes was mainly particulate (Table 5); data collected in both 1981 and 1982 show it was anywhere from 56 to 94 percent particulate phosphorus (Table 5). This hypolimnetic phosphorus did not appear to be transferred to the surface waters.

The data from Hasse Lake were also included with this set. Hasse is a shallow lake which remained weakly thermally stratified until late September (Figure 6). Total phosphorus levels in the epilimnion decreased slowly throughout the summer and there was the suggestion of a small increase in late September (Figure 6). Data collected at Hasse Lake in 1981 show a gradual increase in [TP] below 6 m during June and July. A similar buildup in 1982 would explain the small increase in TP levels in the surface waters in late September. However, further study is needed to explain TP

Table 5. Ratio of total dissolved phosphorus (TDP) to total phosphorus (TP) in the epilimnion of 11 lakes in central Alberta. In the lakes deep enough to remain thermally stratified throughout the summer period, values for below the epilimnion are also given.

Lake	Date	Depth (m)	TDP (mg/m^3)	TDP/TP
Mink	avg. summer	0–5	10	0.39
Baptiste N.	avg. summer	0–5	10	0.24
Wizard	avg. summer	0–5	10	0.22
Amisk N.	avg. summer	0–4	10	0.33
	20/9/82	26	203	0.95
Baptiste S.	avg. summer	0–6	12	0.35
	21/9/82	21	453	0.94
Amisk S.	avg. summer	0–6	10	0.34
	20/9/82	17	134	0.96
	20/9/82	49	198	0.96
Twin	avg. summer	0–4	6.6	0.63
	8/9/82	26	168	0.97
Sauer	avg. summer	0–4	9.3	0.52
	9/6/81	3–7	9.8	0.35
	30/6/81	4–8	17	0.25
	29/7/81	4–7	8.1	0.23
	23/8/82	10	19	0.21
Eden	avg. summer	0–3	6.4	0.38
	3/6/81	5–8	4.5	0.13
	6/7/81	6–9	7.4	0.36
	6/7/81	9–12	9.4	0.12
	23/8/82	11	8.0	0.06
Peanut	avg. summer	0–4	9.4	0.54
	22/8/82	10	57	0.44
Hasse	avg. summer	0–4	9.4	0.48

Table 6. Increase in total phosphorus (TP) in the hypolimnion of four deep lakes during the summer 1982 and average summer euphotic chlorophyll (1980–1982) expressed on a volumetric (mg/m^3) and areal (mg/m^2) basis.

Lake	Change in TP ($mg/m^2/day$) Avg.	Change in TP ($mg/m^2/day$) Range	Chlorophyll *a* (mg/m^3)	Chlorophyll *a* (mg/m^2)
Baptiste S.	14.3	10.3–17.8	30	104
Amisk S.	8.0	5.0–14.4	19	87
Amisk N.	6.2	3.6–8.4	17	73
Twin	3.5	2.8–4.4	1.8	15

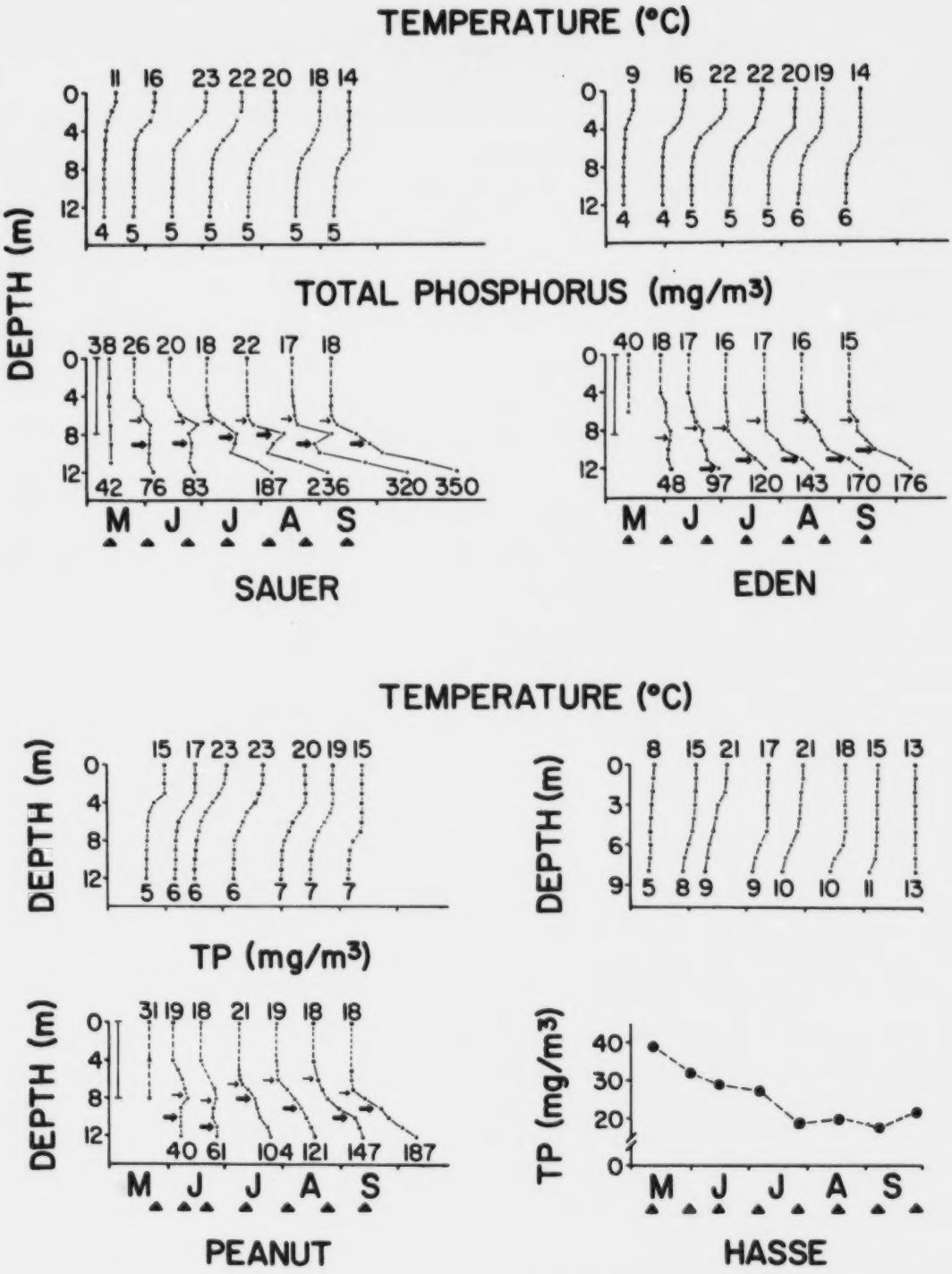

Figure 6. Temporal variation in temperature and the concentration of total phosphorus (TP) in four lakes in central Alberta in 1982. Three lakes were deep enough to remain thermally stratified throughout the study and in these lakes the euphotic zone (indicated by I) extended into the hypolimnion. Light arrows (→) and dark arrows (↠) indicate the depths where the dissolved oxygen concentrations were 1 and 0 mg/L, respectively. For Hasse Lake, the concentration of total phosphorus (TP) in the euphotic zone (avg. depth 6.5 m) are presented. Triangles (▲) indicate sampling dates.

dynamics in this lake. (Complete temperature and phosphorus data for Sauer, Eden, Peanut, and Hasse lakes are in Tables 21, 22, 25, 26, 33, 34, 37, and 38).

6.5 PHOSPHORUS–NITROGEN–CHLOROPHYLL RELATIONSHIPS

The ratios of TN to TP varied from 22 to 79 in the study lakes (Table 7). Thus, TP is likely the nutrient controlling productivity in these lakes (Smith 1982). Changes in TP levels in the euphotic zone were rapidly translated into chlorophyll biomass. In half the study lakes, notably the shallow lakes and the deep lakes where the euphotic zone extended into the hypolimnion, there were significant correlations between TP and Chl *a* levels in the euphotic zone (Table 8). Because only a small number of points ($n = 7$) were used in the correlations in Table 8, overall trends could not be evaluated from individual correlation coefficients. To test whether [TP] and [Chl *a*] were related in all 12 lakes, the probabilities were combined following a technique outlined in Sokal and Rohlf (1981, Box 18.1). Total phosphorus and Chl *a* levels were correlated on a day–to–day basis within lakes (X^2–test, $P < 0.005$). However, [TP] and [TN] were not consistently positively correlated in the study lakes (Table 8). As well, [TN] and [Chl *a*] were positively correlated in only nine of the 12 lakes and the relationships were weaker than for [TP] and [Chl *a*] (Table 8) (TP, Chl *a*, and TN data are in Tables 29 to 40, 41, and 42, respectively).

6.6 SEDIMENTS AS A PHOSPHORUS SOURCE

In the shallow lakes, intermittent increases in TP in the surface waters were associated with periods of partial mixing. The dynamics of TP in these lakes were similar to those described for other north temperate shallow lakes (e.g., Stewart and Markello 1974; Larsen et al. 1975, 1981; Stefan and Hanson 1981). Laboratory studies have shown that the rate of phosphorus release from sediments is influenced by the temperature of the water overlying the sediments, by lake productivity (and hence the rate of sedimentation of organic material), and by sediment type (Olsen 1958; Morris and Stumm 1967; Holdren and Armstrong 1980). However, phosphorus release rates under field conditions cannot be predicted at present.

During summer, DP accumulated in the hypolimnion of the deep lakes

Table 7. Average ratio (plus range from June until September) of total nitrogen (TN) to total phosphorus (TP) in the epilimnion of the lakes studied in central Alberta in 1982.

Lake	TN:TP	Range
Mink	31	17-43
Lessard	53	49-58
Baptiste N.	25	24-26
Wizard	22	21-25
Amisk N.	29	23-35
Baptiste S.	34	25-40
Amisk S.	28	21-36
Twin	27	18-41
Sauer	61	47-75
Eden	41	32-54
Peanut	79	66-91
Hasse	57	45-74

Table 8. Correlations (*r*) between total phosphorus (TP), total nitrogen (TN), and chlorophyll *a* (Chl *a*) concentrations in the euphotic zone of the study lakes. All data were transformed to $\log_{10}$ prior to these analyses. Significant correlations are indicated by *($P < 0.05$) or **($P < 0.01$).

	Variables		
Lake	TP–Chl *a*	TN–Chl *a*	TN–TP
Mink	0.90**	0.81*	0.83*
Lessard	0.86*	0.53	0.29
Baptiste N.	0.62	0.18	0.07
Wizard	0.81*	0.85*	0.84*
Amisk N.	0.19	0.57	0.84*
Baptiste S.	0.74	0.24	0.21
Amisk S.	0.02	0.17	0.72
Twin	0.57	0.39	0.02
Sauer	0.84*	0.30	0.30
Eden	0.98**	0.24	0.25
Peanut	0.37	0.42	0.48
Hasse	0.95**	0.51	0.48

where the euphotic zone did not extend into the hypolimnion. The following three separate lines of evidence suggest that this buildup was of sediment origin and not from the mineralization in the hypolimnion of organic matter sinking out of the epilimnion:

1. The phosphorus increase started at the sediment–water interface and moved up the water column as dissolved oxygen was depleted (Figure 5).
2. There is no similar hypolimnetic increase in deep lakes which have well–oxygenated hypolimnia (e.g., Bodensee [Wagner 1967]; Horw Bay, [Bloesch 1974]). This is illustrated in Table 9 with data on temporal changes in TDP in Bob Lake, an oligotrophic lake situated on the Precambrian Shield. (TP data for Bob Lake are in Prepas and Rigler 1982). Hypolimnetic mineralization in Bob Lake should be similar to Twin Lake, the unproductive deep lake in this study. Both Twin and Bob lakes have similar morphometry (mean depths 16 and 18 m, respectively) and biomass (mean summer [Chl *a*] in the euphotic zone was 1.2 mg/L, in both lakes) (the Bob Lake data are from Dillon and Rigler 1974a, 1974b). However, DP increased in the hypolimnion of Twin Lake (Figure 5) and did not increase in Bob Lake (Table 9).
3. In Horw Bay, a deep mesotrophic lake, there was no noticeable mineralization of particulate phosphorus in the water column (Bloesch 1974).

Although there was no evidence in this study that the hypolimnetic accumulation of DP was associated with mineralization in the water column, it was highly correlated with the average amount of organic material in the euphotic zone of lakes (Table 6). Thus, release rates from the sediments may be influenced by lake productivity. The DP which accumulated in the hypolimnion of the deep lakes was not transferred into the epilimnion for most of the summer. Phosphorus was transported from the hypolimnion to the epilimnion only when DP had accumulated at the top of the hypolimnion and the thermocline was depressed.

Table 9. Vertical distribution of total dissolved phosphorus (mg/m^3) in Bob Lake, 1978.

Depth	Date					
m	13/3	7/5	7/6	30/6	28/7	3/9
0–5	4.4	3.0	2.0	2.6	2.5	2.6
5–15	2.8	3.0	2.1	2.8	2.9	2.8
15–25	2.6	2.8	2.3	2.9	3.0	3.0
25–35	2.6	2.6	2.4	2.9	3.1	3.2
35–45	3.8	2.7	2.3	3.0	3.2	3.3

During the summer, particulate phosphorus increased in the hypolimnion of the lakes which were deep enough to remain thermally stratified and where the euphotic zone extended into the hypolimnion (Figure 6). These lakes were similar to the artificially eutrophied lakes in northwestern Ontario (Schindler et al. 1971, 1973; Schindler and Fee 1974). In the latter, phosphorus buildup in the hypolimnion was particulate, even when orthophosphate was injected directly into the hypolimnion. The particulate phosphorus which accumulated in the hypolimnion of the lakes in the present study was probably a combination of bacteria and algae, some of which were capable of photosynthesis. Photosynthesis was clearly taking place, since there was no depletion of dissolved oxygen in the portion of the hypolimnion which was within the euphotic zone (Figure 6). Further studies are required to determine the nature of this particulate material. When the thermocline was depressed in fall, surface water [TP] did not increase in these lakes. Thus, the TP which accumulated in the hypolimnion of these lakes might not be available to biota living in the surface waters. Sediment release rates were not calculated for these lakes because both release and uptake of dissolved phosphorus were occurring in the hypolimnion.

The data collected in this study suggest that lake sediments can be a source of phosphorus as long as there are low levels of dissolved oxygen in the hypolimnion. However, more information is needed on the factors controlling release rates of phosphorus from the sediments before this input can be included in whole-lake nutrient budgets. It is also clear that seasonal phosphorus dynamics can have a strong influence on chlorophyll biomass, contrary to patterns observed by Stewart and Markello (1974). Thus, these seasonal fluctuations in surface water TP levels have important implications for lake management.

7. THE IMPORTANCE OF LARGE ZOOPLANKTON IN THE TOTAL PHOSPHORUS POOL

7.1 CALIBRATION OF 250-μM TOW NETS

The Schindler-Patalas trap fitted with 250-μm netting collected more PP per unit volume in 27 out of 28 comparisons and more ZP in 20 out of 23 comparisons made (Table 10). The data were quite variable, perhaps because the trap sampled less than a third of the volume of water sampled by the tow net in each set of comparisons and may have been more affected by plankton patchiness. On average, the Schindler-Patalas trap collected 20% more phosphorus than the tow net, both for the entire fraction > 250 μm and the animal fraction > 250 μm. The distance which a net is pulled through the water and lake productivity may affect net efficiency (e.g., Smith et al. 1968). Since the plankton tows in this study were vertical, we tested whether depth had an effect on net efficiency. Profiles were collected from six lakes and divided into a shallow portion (extending to 4 m on average) and a deep portion (extending from 4 to 8 m on average) (method of calculation outlined in Prepas and Rigler 1982). These samples were representative of the depths sampled in most lakes during 1981 and 1982. Tow depth did not affect net efficiency for collecting PP >250 μm and ZP > 250 μm (signed-rank test, $P>>0.10$, $n=11$ and 7, respectively). In addition, net efficiency in the lake with the highest mean summer [Chl *a*] (Baptiste S.) was similar to the least productive lake (Twin) in our study (Table 10). Because there were no trends with depth of tow or level of lake productivity, all phosphorus values derived by the use of a tow net were increased by 20%. The tow net efficiencies for the Alberta lakes were lower than reported for a lake on the Precambrian Shield (Prepas and Rigler 1982). Thus, tow net efficiencies calculated in one geographic area may not be generally applicable.

As expected, a substantial fraction of PP was in the fraction which was > 80 μm and less than 250 μm. The trap fitted with a 250-μm net collected less material than the trap fitted with an 80-μm net on six out of seven occasions: the average ratio for PP was 0.69 (range 0.3 to 1.2) and for ZP it was 0.75 (range 0.5 to 1.2). Similarly, the 250-μm tow net collected less PP than the 80-μm tow net, but

Table 10. Ratios of particulate phosphorus > 250 µm collected by the Schindler–Patalas trap to that collected by a tow net in nine lakes in central Alberta. Ratios for the entire sample and the animal fraction are given. The range is indicated in brackets. Samples were collected in 1981 and 1982 and the results are pooled for each lake. The number of profiles (n) used in each ratio is indicated.

		Fraction Analysed	
Lake	n	Entire	Animal
Amisk N.	5	1.2 (1.0–1.4)	1.0 (0.6–1.2)
Amisk S.	5	1.2 (1.0–1.5)	1.0 (0.8–1.2)
Baptiste S.	3	1.6 (1.0–2.0)	1.3 (0.6–2.2)
Eden	5	1.1 (0.8–1.4)	1.3 (1.1–1.4)
Ethel*	1	1.2	ND
Moore*	2	1.2 (1.1–1.2)	ND
Sauer	4	1.3 (1.0–1.6)	1.5 (1.2–2.0)
Tucker*	1	1.1	ND
Twin	2	1.7 (1.3–2.2)	1.2 (1.1–1.4)
	Average	1.2	1.2

* Data collected in conjunction with Alberta Environment.

interestingly, more PP in the animal fraction (Table 11). The differences between the ratios of PP collected with the 250-µm and 80-µm nets and the ratios of ZP collected with the 250-µm and 80-µm nets on the 15 occasions when duplicate samples were taken were highly significant (signed-rank test, $n=15$, $P>>0.01$). Thus, large zooplankters were selectively able to avoid the opening of an 80-µm net (Table 11). The 250-µm tow net chosen for this study was equally efficient at collecting large phytoplankton and zooplankton. However, for equal efficiencies with a smaller mesh size, the net design should be modified. These comparisons also demonstrate that the choice of mesh size can affect the relative contribution of PP to the TP pool.

7.2 PHOSPHORUS IN THE > 250 µM FRACTION

The data collected in 1980 on the deep lakes suggest that PP > 250 µm was largely concentrated in the euphotic zone (Table 12). Thus in Amisk N., Amisk S., and Baptiste S. lakes, where the euphotic zone was limited to the epilimnion, PP > 250 µm was also concentrated in the epilimnion throughout most of the sampling period (as illustrated in Figure 7). However, in Hubbles, Narrow, and Twin lakes where the euphotic zone extended below the epilimnion, concentrations of PP > 250 µm were highest in the epilimnion during spring, and then the maxima descended during summer (as illustrated in Figure 8). Thus, when the euphotic zone extended below the epilimnion in summer, a PP (> 250 µm) maximum developed in the deeper part of the euphotic zone.

These results on vertical distribution of PP > 250 µm are only partially consistent with the data collected on Bob Lake, Ontario (Prepas and Rigler 1982). In Bob Lake, PP > 250 µm was also concentrated in the euphotic zone during summer. However, concentrations of PP > 250 µm were highest in the epilimnion of Bob Lake, even though the euphotic zone extended well below the epilimnion. An explanation for the differences in the vertical distribution of PP > 250 µm in Bob Lake and lakes like Hubbles lies in the chemical conditions in the hypolimnia of the two lake types. The hypolimnion of Bob Lake was well oxygenated, and TP levels were only slightly higher in the hypolimnion than in the epilimnion (Prepas and Rigler 1982). However, most deep lakes in central Alberta are partially meromictic. In these lakes, dissolved oxygen levels

TABLE 11. Ratios of particulate phosphorus collected by tow nets made with 250- and 80-µm mesh. Average ratios for the entire sample and animal fraction are given. The number of profiles (n) used to calculate the average ratio and the range of ratios in each group are indicated. Samples were collected from nine lakes in central Alberta on 15 separate occasions during 1981 and 1982.

Fraction analysed	n	250/80 µm	Average Range
Entire	20	0.8	0.4 – 1.3
Animal	16	1.1	0.8 – 1.5

Table 12. Vertical variation in particulate phosphorus >250 µm (PP>250 µm) in 1980 in eight lakes in central Alberta. Data are expressed in two ways: as phosphorus concentration and as the percent of the total phosphorus pool (TP) in the fraction >250 µm. Depth indicates where tow began.

Lake	Date	Depth (m)	PP>250 µm (mg/m³)	PP>250 µm / TP X100
Amisk N.	14/5	3	6.39	8.75
		10	3.34	4.06
		20	1.88	2.05
	11/6	7	11.42	20.28
		12	7.99	11.27
		20	5.02	5.46
	2/7	4	7.50	18.98
		10	4.20	8.48
		15	3.07	3.91
	22/7	4	8.66	19.05
		10	5.66	11.02
		15	4.45	5.22
	12/8	6	5.40	13.99
		10	4.80	11.71
		15	2.88	3.63
Amisk S.	14/5	3	9.67	12.26
		10	5.00	5.77
		20	2.52	2.62
	11/6	6	12.36	22.74
		11	9.38	15.11
		20	4.92	5.89
	2/7	4	7.20	17.35
		10	4.80	10.17
		15	3.72	5.27
	22/7	3	3.18	8.37
		9	5.54	12.69
		15	3.66	4.95
	12/8	5	6.68	16.46
		10	6.50	12.95
		15	3.77	4.59

continued ...

Table 12. Continued.

Lake	Date	Depth (m)	PP>250 µm (mg/m³)	PP>250 µm / TP X 100
Baptiste N.	13/5	3	1.12	1.95
	10/6	4	7.63	14.52
	3/7	4	8.12	14.44
	23/7	4	12.65	13.73
	13/8	4	8.02	8.66
Baptiste S.	13/5	3	1.32	1.68
		6	0.80	0.98
		15	1.21	1.12
	10/6	8	3.56	7.18
		12	2.80	4.32
		15	2.24	2.76
	3/7	6	7.08	15.20
		9	4.08	7.52
		15	3.12	3.17
	24/7	4	11.33	19.80
		9	8.08	12.40
		15	5.29	4.42
	13/8	8	4.32	6.60
		11	3.48	4.50
		15	8.04	6.48
Hubbles	6/5	4	9.24	25.43
		5*	8.52	23.92
		10	5.64	17.23
	19/6	3	1.20	6.85
		8	5.88	30.03
		10*	4.74	21.00
		12	4.92	15.91
	10/7	4	0.40	2.63
		7	0.68	4.03
		9*	2.16	10.61
		10	7.34	22.70
		15	3.89	9.05
	30/7	5	0.46	2.62
		9	5.62	17.39
		12	3.40	8.10

continued ...

Table 12. Continued.

Lake	Date	Depth (m)	PP>250 µm (mg/m³)	PP>250 µm / TP X 100
Hubbles	18/8	5	0.94	5.39
		9	2.57	9.56
		10*	2.66	9.18
		15	3.54	7.43
	30/9	7	0.36	2.16
		15	3.36	11.03
Nakamun	12/5	5	18.60	27.89
	19/6	5	28.92	22.61
	10/7	4	39.48	23.89
	30/7	5	19.50	8.21
	18/8	4	5.63	2.86
Narrow	16/6	4	0.06	0.42
		9	2.03	12.82
		12*	2.08	13.26
		18	2.20	14.47
	7/7	4	0.66	4.69
		10	2.05	12.77
	28/7	5	0.66	5.52
		10	2.11	14.06
		11*	2.16	14.31
		15	2.69	16.93
		20	1.66	9.24
	30/8	6	0.25	2.28
		9	0.85	7.00
		13*	1.27	9.72
		15	2.22	14.68
Twin	9/5	5	2.04	9.79
		8	1.80	7.66
		15	0.86	3.46
	23/5	10.4	0.90	6.62
	5/6	6	4.49	23.52
		9	4.14	21.08
		15	2.54	12.19
	24/6	3	2.40	13.64
		6*	1.80	11.69
		9	1.56	11.50
		20	0.91	3.13

continued ...

Table 12. Concluded.

Lake	Date	Depth (m)	PP>250 µm (mg/m³)	PP>250 µm / TP X100
Twin	15/7	3	0.07	0.59
		8	1.19	10.36
		15	1.80	9.28
	7/8	5	0.34	3.42
		8.5*	0.62	6.22
		10	1.04	10.36
		15	1.58	8.99
	25/8	5	2.06	18.13
		10	1.37	13.60
		15	1.31	6.89

* Interpolated values.

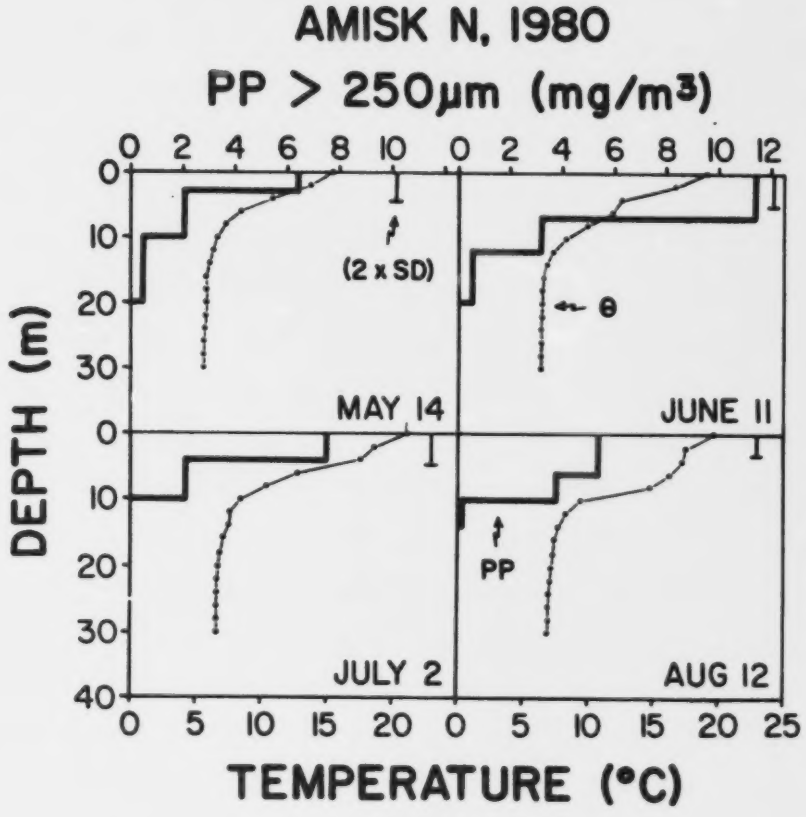

Figure 7. Vertical distribution of particulate phosphorus (PP) > 250 µm and temperature (θ) in Amisk N. Lake, 1980. The approximate depth of the euphotic zone is indicated (2 x SD).

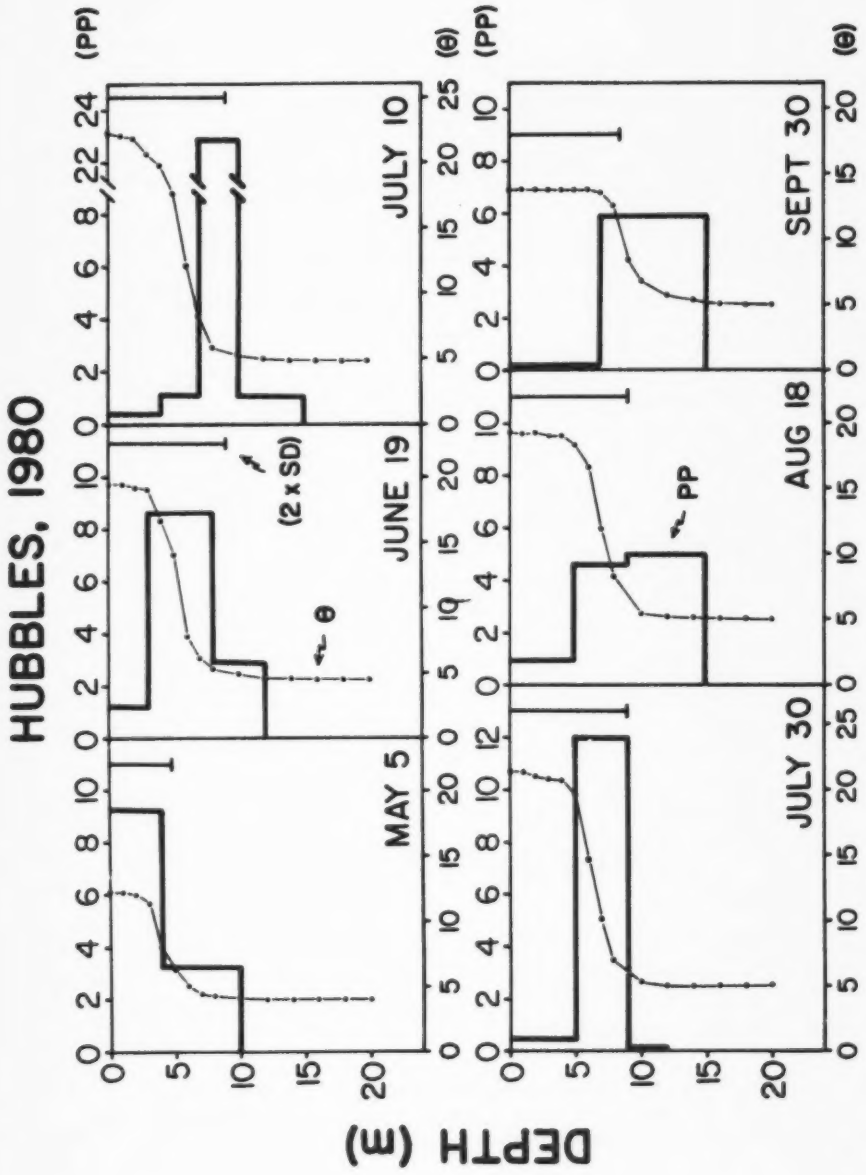

Figure 8. Vertical distribution of particulate phosphorus (PP) > 250 µm (mg/m³) and temperature (θ) (°C) in Hubbles Lake, 1980. The approximate depth of the euphotic zone is indicated (2 x SD).

are low in the hypolimnion and concentrations of TP < 250 µm are often several-fold higher in the hypolimnion than in the epilimnion. In some of these lakes, the phytoplankton (estimated by Chl *a*) aggregate below the epilimnion (Section 4.2).

In 1981, we investigated whether the phytoplankton and PP > 250 µm were distributed in similar parts of the water column in deep lakes in this study (mixing patterns in Table 2; PP > 250 µm in Table 13). Once again, PP > 250 µm was concentrated in the euphotic zone of the study lakes (Figures 9 and 10). In Amisk N., Amisk S., and Baptiste S. lakes, the euphotic zone was limited to the epilimnion for a second year. In these lakes, concentrations of Chl *a* and PP > 250 µm were also highest in the epilimnion (illustrated in Figure 9). In contrast, in Hubbles, Narrow, Roi, and Sauer lakes the euphotic zone extended into the hypolimnion. In these four lakes, the highest concentrations of Chl *a* and PP > 250 µm were below the epilimnion throughout the summer period (illustrated in Figure 10). Thus, in summer in individual lakes, the maximum concentrations of chlorophyll and PP > 250 µm were in the same stratum, although the data are only approximate. The comparison between Bob Lake and the partially meromictic lakes in central Alberta cannot be completed since data on the vertical distribution of Chl *a* are not available for Bob Lake.

Over two years (1981 and 1982), samples were collected from 17 lakes to estimate the contribution of PP > 250 µm to the TP pool in the euphotic zone. In the second year, the contribution of ZP > 250 µm to the TP pool in the euphotic zone, was also estimated. In the open-water season, the contribution of PP > 250 µm to the TP pool varied as much as from 3 to 31% in individual lakes (Tables 13 and 14). The temporal patterns were variable, with no clear trends. In the deep lakes studied in 1982 and Eden Lake in 1981, PP > 250 µm was a relatively small portion of the TP pool (0 to 5%) early in the season, then increased to maximum levels (17 to 23%) in mid-summer (Tables 13 and 14). However, in the other deep lakes studied in 1981, and over all years in the shallow lakes, no consistent patterns emerged (Tables 12, 13, and 14). Seasonal trends in the contribution of ZP > 250 µm to the TP pool were similar to PP > 250 µm in most lakes (Table 14). The seasonal changes in PP > 250 µm and ZP > 250 µm were apparently independent of changes in either TP < 250 µm or Chl *a* levels (Figure 11).

Table 13. Phosphorus in the fraction >250 µm (PP > 250 µm) and percent of the total phosphorus pool (TP) in the fraction > 250 µm in the euphotic zone of the 15 lakes studied in 1981. Depth indicates where tow began.

Lake	Date	Depth (m)	PP>250 µm (mg/m³)	PP>250 µm X 100 / TP
Amisk N.	15/6	5	5.54	14.84
	13/7	4	10.36	23.78
	10/8	3	3.95	11.40
Amisk S.	15/6	6	5.09	14.76
	13/7	4	7.60	19.19
	10/8	4	5.10	12.56
Baptiste N.	16/6	5	2.28	14.73
	14/7	5	6.94	12.61
	12/8	2	2.40	3.95
Baptiste S.	16/6	6	2.06	6.30
	14/7	3	9.08	20.32
	12/8	2	1.20	2.83
Eden	6/5	6	0.70	2.38
	3/6	8	1.72	6.58
	6/7	9	2.58	7.13
	21/7	6	3.84	19.35
Hasse	6/5	5	7.02	20.63
	3/6	8	4.46	18.48
	24/6	8	2.89	11.43
	22/7	8	4.32	16.48
Hubbles	4/5	10	6.31	15.62
	26/5	8	5.28	19.64
	24/6	8.5	9.36	31.14
	17/7	9	4.44	16.86
	5/8	6	0.62	2.84
Mink	5/5	5	7.56	23.43
	1/6	5	8.23	26.10
	23/6	5	2.76	21.13
	20/7	5	6.78	8.06
Nakamun	20/5	4	0.32	0.41
	10/6	1.5	0.70	0.69
	22/6	1.2	7.49	3.55
	21/7	0.6	4.69	2.73
	5/8	2	7.37	5.34
Narrow	19/5	15	2.21	14.34
	10/6	11	1.91	13.93
	27/7	12	0.29	2.28

continued ...

Table 13. Concluded.

Lake	Date	Depth (m)	PP>250 µm (mg/m³)	PP>250 µm / TP X 100
Roi	7/5	8	0.68	4.83
	9/6	8	3.28	19.43
	30/6	7	1.80	11.92
	29/7	9	1.25	6.63
Sauer	7/5	4	1.19	3.48
	9/6	7	2.69	6.92
	30/6	8	3.23	7.13
	29/7	7	2.00	3.91
Star	5/5	5.5	3.97	12.11
	1/6	5	4.10	16.33
	23/6	5	6.19	20.92
	20/7	4	4.63	19.51
Twin	11/5	9	2.14	11.60
	8/6	11	2.32	14.76
	1/7	12	1.99	14.02
Wizard	2/6	5	9.83	27.74
	1/7	5	4.01	11.07
	28/7	2.5	1.19	2.02
	12/8	2	1.74	2.75

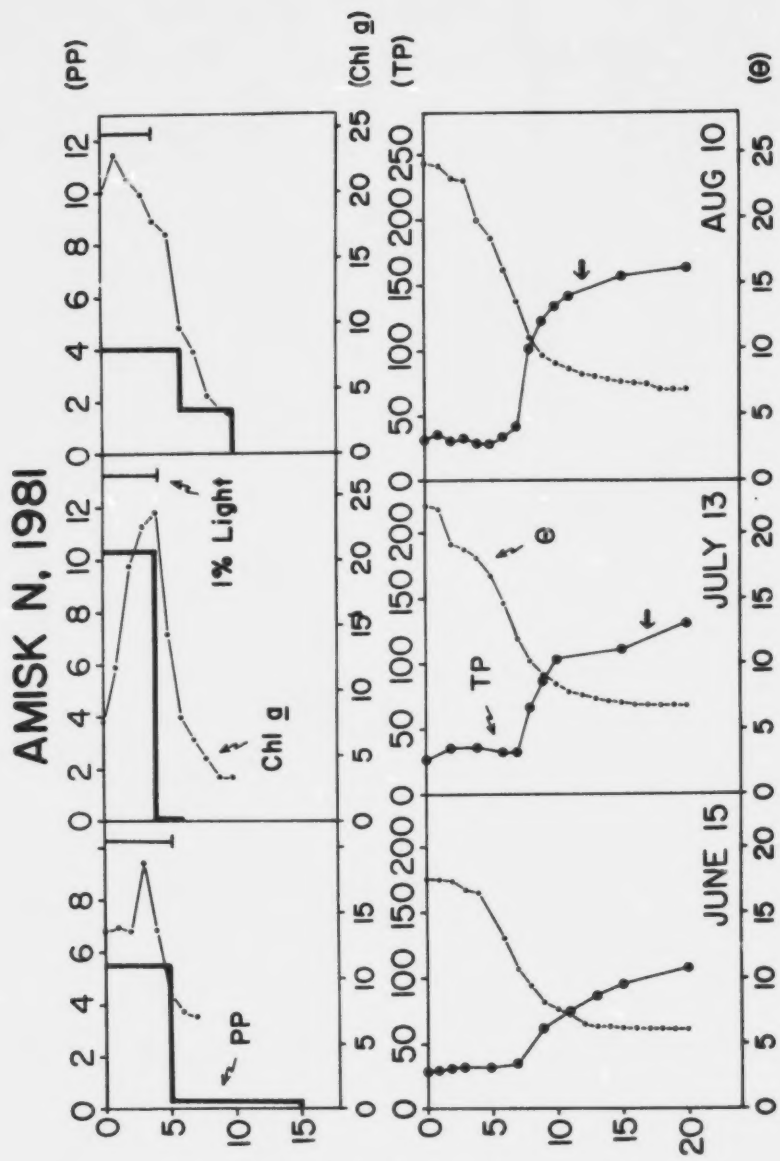

Figure 9. Vertical distribution of particulate phosphorus > 250 µm (PP) (mg/m³), chlorophyll *a* (Chl *a*) (mg/m³), total phosphorus < 250 µm (TP) (mg/m³), and temperature (θ) (°C) in Amisk N. Lake, 1981. The depth of 1% light is indicated.

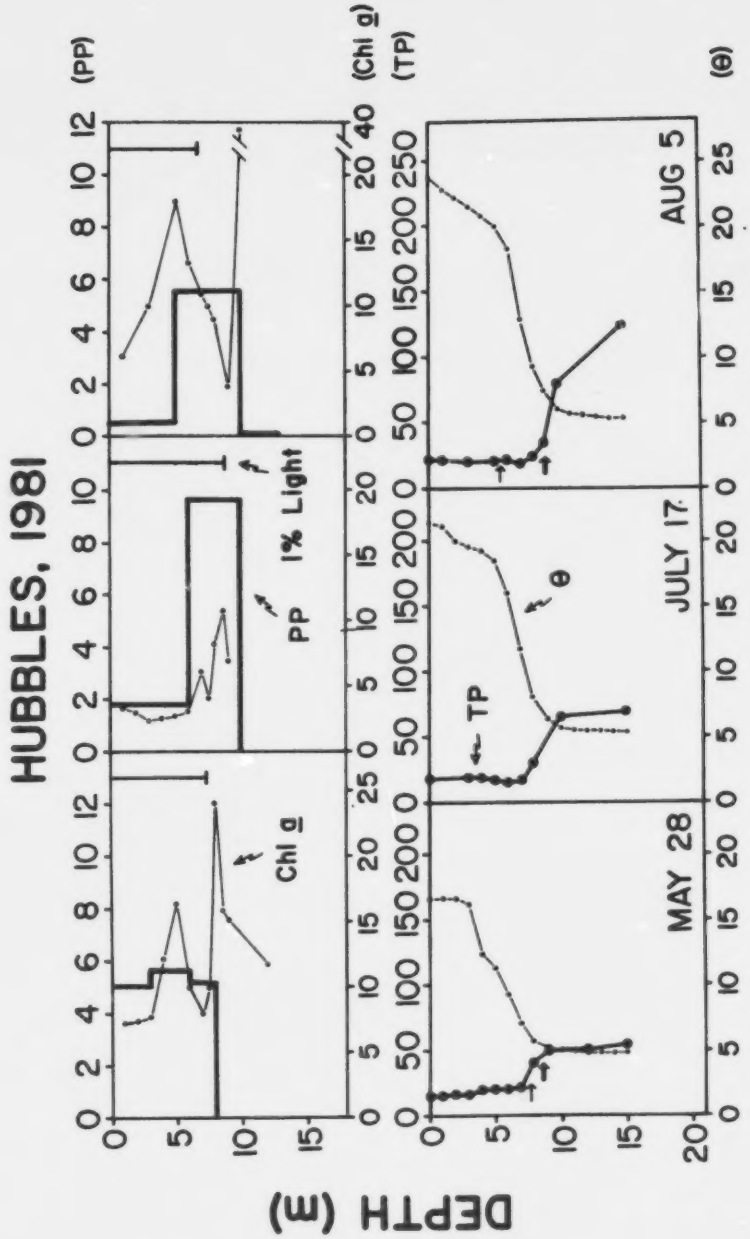

Figure 10. Vertical distribution of particulate phosphorus > 250 µm (PP) (mg/m³), chlorophyll *a* (Chl *a*) (mg/m³), total phosphorus < 250 µm (TP) (mg/m³), and temperature (θ) (°C) in Hubbles Lake, 1981. The depth of 1% light is indicated.

Table 14. Particulate phosphorus in the fraction >250 µm (PP>250µm) and in the animal portion of this fraction (ZP>250µm) and percent of the total phosphorus pool (TP) in the fraction >250 µm in the euphotic zone of the 12 lakes studied in 1982. Lakes are either thermally mixed (M) or stratified (S). Depth indicates where tow began.

Lake	Date	Depth (m)	Thermal Regime	PP>250µm (mg/m³)	ZP>250µm (mg/m³)	PP>250µm TP x100	ZP>250µm TP x100
Amisk N.	17/5	5		1.32	1.07	1.66	1.35
	6/6	8		5.33	3.34	8.50	5.32
	27/6	7		**7.43	**4.58	**14.49	**8.93
	19/7	5	S	*7.68	*6.42	*19.26	*16.10
	9/8	4		*6.22	*4.68	*14.84	*11.16
	31/8	7		*5.77	*4.54	*17.14	*13.48
	20/9	4		5.12	3.23	11.05	6.97
Amisk S.	17/5	6		1.73	1.51	2.01	1.76
	7/6	7		5.32	2.87	8.82	4.76
	28/6	6		**6.68	**4.15	**13.58	**8.44
	19/7	5	S	*6.02	*5.29	*16.99	*14.93
	9/8	4.5		*9.16	*5.74	*19.55	*12.25
	31/8	7		*6.40	*3.76	*17.93	*10.53
	20/9	5		3.08	2.28	7.20	5.33
Baptiste N.	18/5	3		1.26	1.19	1.14	1.08
	8/6	6		1.58	1.03	3.20	2.08
	29/6	4		*3.48	*2.39	*6.73	*4.62
	20/7	4	M	*9.84	*8.98	*14.99	*13.68
	10/8	3		*4.99	*3.89	*7.44	*5.80
	1/9	4		*7.64	*6.98	*7.90	*7.22
	21/9	4		12.96	13.60	13.38	14.04
Baptiste S.	18/5	4		0.46	0.23	0.38	0.19
	8/6	6		0.29	0.19	0.54	0.36
	28/6	4		*2.66	*1.92	*5.14	*3.71
	20/7	6	S	*9.24	*7.64	*23.25	*19.22
	10/8	3.5		*10.78	*9.26	*22.51	*19.34
	1/9	5		*7.13	*7.18	*19.25	*19.39
	21/9	6		4.08	3.86	8.83	8.36

continued...

Table 14. Continued.

Lake	Date	Depth (m)	Thermal Regime	PP>250µm (mg/m³)	ZP>250µm (mg/m³)	PP>250µm TP x100	ZP>250µm TP x100
Eden	12/5	6		0.19	ND	0.44	ND
	1/6	8		1.32	0.84	4.73	3.01
	22/6	8		*4.37	*2.83	*18.54	*12.01
	13/7	9	S	*3.72	*2.74	*16.30	*12.01
	4/8	7.5		*4.38	*3.88	*18.58	*16.45
	23/8	8		*3.31	*3.72	*15.75	*17.71
	14/9	8		*2.62	*2.51	*14.70	*14.08
Hasse	11/5	7		0.01	ND	0.02	ND
	31/5	6		1.26	0.41	3.80	1.24
	15/6	7		*3.28	*1.70	*10.19	*5.28
	6/7	7	?	*4.13	*3.22	*13.14	*10.24
	27/7	6.5		*5.40	*3.86	*23.89	*17.08
	17/8	6		*2.90	*2.26	*12.66	*9.87
	7/9	7		*2.71	*2.26	*13.28	*11.07
	27/9	4.5		2.69	2.21	11.12	9.14
Lessard	25/5	4		4.56	1.90	10.01	4.17
	9/6	4		6.43	3.40	18.30	9.68
	21/6	3		*1.24	*0.55	*5.73	*2.54
	3/8	3.5	M	*7.01	*5.04	*19.15	*13.77
	24/8	3		*6.94	*3.14	*21.39	*9.68
Mink	18/5	7		1.20	1.42	2.17	2.57
	31/5	6		3.91	3.44	10.89	9.58
	15/6	7		**8.53	**6.17	**23.94	**17.32
	6/7	7	M	*2.92	*2.06	*7.56	*5.33
	27/7	5		*3.37	*2.39	*9.55	*6.78
	17/8	3		*4.54	*3.29	*5.52	*4.00
	7/9	3		*9.02	*6.11	*12.83	*8.69

continued...

Table 14. Concluded.

Lake	Date	Depth (m)	Thermal Regime	PP>250µm (mg/m³)	ZP>250µm (mg/m³)	PP>250µm TP x100	ZP>250µm TP x100
Peanut	25/5	8		0.17	0.14	0.53	0.44
	9/6	8		1.56	1.07	4.80	3.30
	21/6	9		*5.26	*3.96	*16.56	*12.47
	3/8	8	S	*3.40	*2.81	*13.65	*11.28
	24/8	7.5		*3.17	*2.90	*13.39	*12.25
	13/9	8		*4.80	*4.13	*20.60	*17.72
Sauer	12/5	6		<0.05	0.05	0.09	
	1/6	7		1.33	1.00	3.51	2.64
	22/6	8		*6.04	*4.08	*15.31	*10.34
	13/7	6	S	*2.33	*1.68	*10.08	*7.59
	4/8	7.5		*5.33	*4.30	*17.69	*14.27
	23/8	8		*3.92	*3.25	*14.56	*12.07
	14/9	7.5		*3.66	*3.31	*17.13	*15.50
Twin	26/5	8		1.25	0.84	3.82	2.56
	14/6	9		3.00	2.28	18.40	13.99
	5/7	5		*3.29	*2.65	*23.18	*18.68
	26/7	5	S	*1.80	*1.30	*12.76	*9.22
	18/8	5		*2.62	*1.80	*19.52	*13.41
	8/9	6		*2.40	*2.04	*21.82	*18.54
Wizard	26/5	5		3.70	2.04	7.00	3.86
	14/6	6		3.77	2.10	9.62	5.36
	5/7	5		*4.13	*3.41	*8.24	*6.80
	26/7	3	M	*1.06	*0.60	*2.04	*1.15
	18/8	3		*0.84	*0.46	*1.50	*0.82
	8/9	2.5		*0.94	*0.53	*1.38	*0.78
	27/9	3		1.00	0.68	1.71	1.16

* used in summer average
** not used in summer average due to analytical problems

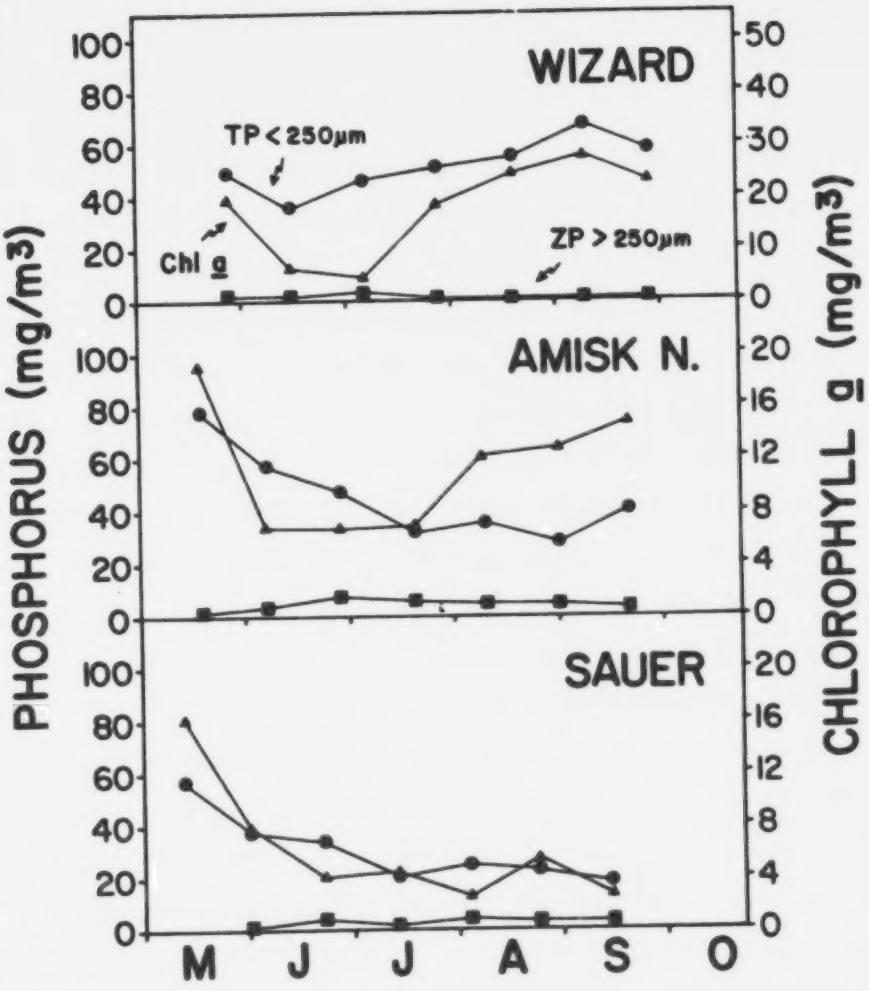

Figure 11. Temporal variation in the concentration of total phosphorus (TP) < 250 µm, chlorophyll *a* (Chl *a*), and particulate phosphorus in animals (ZP) > 250 µm in three lakes in central Alberta in 1982.

During summer, PP > 250 μm was a much more variable portion of the TP pool in most of the study lakes than in Bob Lake (Prepas and Rigler 1982). In individual deep lakes, PP > 250 μm varied as much as from 6 to 20% of the TP pool in the euphotic zone (Tables 13 and 14). In the shallow lakes, the contribution of PP > 250 μm in the euphotic zone in summer varied from 8 to 26% in Nakamum in 1981, to 1 to 7% in Wizard in 1982 (Tables 13 and 14). Thus, to estimate the contribution of PP > 250 μm to the summer TP pool, samples should be collected over several dates

In individual lakes, the average summer contribution of PP > 250 μm to the TP Pool in the euphotic zone varied from 3 to 19% (Table 4). This ratio also varied for individual lakes from year to year. In deep lakes, PP > 250 μm averaged 15% (±0.9; $\bar{X}$±*s.e.*) of the TP pool, whereas in shallow lakes it averaged 10% (± 1.9) (Table 4). The mean values for deep and shallow lakes are significantly different (Wilcoxon test, $n_1 = 8$, $n_2 = 17$, $P < 0.05$). This difference between deep and shallow lakes was even clearer in the animal fraction: in the deep lakes ZP > 250 μm was 12 to 15% (14 ± 0.5) of the TP pool, whereas in the shallow lakes it was 2 to 9% (6 ± 1.4) of the TP pool (Table 15). The animal fraction was a major portion of PP > 250 μm; ZP > 250 μm averaged 77% of PP > 250 μm, 81% in deep lakes, and 71% in shallow lakes. Thus, both PP > 250 μm and ZP > 250 μm tended to be a larger portion of the TP pool in deep as compared with shallow lakes.

Also tested was the possibility of significant relationships between mean summer Chl *a*, as an estimate of lake productivity, and either absolute or relative amounts of PP > 250 μm and ZP > 250 μm (data in Tables 2, 15, and 16). The fraction of the TP pool incorporated in PP > 250 μm was negatively correlated with [Chl *a*] ($r = -0.52$, $n = 27$, $P < 0.01$) and with the fraction of the TP pool incorporated in ZP > 250 μm ($r = -0.63$, $n = 12$, $P = 0.03$). Particulate phosphorus > 250 μm and ZP > 250 μm (in mg/m³) were not significantly related to [Chl *a*], although these relationships were positive, rather than negative ($r = 0.15$, $n = 27$, $P = 0.47$; $r = 0.36$, $n = 12$, $P = 0.24$, respectively). Thus, the relative contribution of large particles (PP > 250 μm and ZP > 250 μm) to the TP pool decreased as productivity increased.

Table 15. Percentage of the total phosphorus pool (TP) in the entire fraction > 250 µm (PP > 250 µm) and in the animal portion of this fraction (ZP > 250 µm) for 17 lakes in central Alberta which were sampled in 1981 and 1982. Values are average summer for the euphotic zone. Data are presented in chronological order. Missing data indicated by ND.

Lake	PP>250 µm X 100 / TP	ZP>250 µm X 100 / TP
Amisk N.	16.67	ND
	17.08	13.58
Amisk S.	15.50	ND
	18.16	12.57
Baptiste N.	10.43	ND
	9.26	7.83
Baptiste S.	9.82	ND
	17.54	15.42
Eden	11.02	ND
	16.77	14.45
Hasse	15.46	ND
	14.63	10.71
Hubbles	16.94	ND
Lessard	ND	ND
	15.42	8.66
Mink	18.43	ND
	11.88	8.42
Nakamun	3.00	ND
Narrow	8.10	ND
Peanut	ND	ND
	16.05	13.43
Roi	12.66	ND
Sauer	5.99	ND
	14.95	11.95
Star	18.92	ND
Twin	14.39	ND
	19.32	14.96
Wizard	10.90	ND
	3.29	2.39

Table 16. Spring total phosphorus (TP) and summer TP and summer chlorophyll *a* (Chl *a*) collected in 1982 in 12 Alberta lakes. The spring values are early and late spring, respectively, and the summer values start at either 3 or 6 weeks after ice-out, respectively.

Lake	Spring TP (mg/m^3)	Summer TP (mg/m^3)	Summer Chl *a* (mg/m^3)
Amisk N.	77.1	40.0	9.1
	57.4	31.9	10.6
Amisk S.	84.3	31.1	12.3
	55.0	32.1	15.3
Baptiste N.	109.0	60.6	16.4
	47.8	63.8	18.2
Baptiste S.	119.3	39.9	12.9
	53.0	36.6	14.0
Eden	43.0	20.4	4.1
	26.6	18.1	3.3
Hasse	39.1	23.8	4.5
	31.9	22.2	3.8
Lessard	41.0	25.8	11.1
	28.7	25.2	13.0
Mink	54.1	40.9	12.3
	32.0	46.7	14.3
Peanut	31.9	24.8	5.2
	30.9	21.8	4.6
Sauer	56.6	27.5	4.9
	36.6	23.8	3.8
Twin	31.5	11.2	1.3
	13.3	10.6	1.2
Wizard	49.1	50.9	16.3
	35.4	54.8	18.8

7.3 PHOSPHORUS–CHLOROPHYLL RELATIONSHIP AND PP > 250 µM

If the TP pool is partitioned between plant and animal biomass, then in lakes where the phytoplankton biomass is larger than predicted from the TP pool, the zooplankton biomass should be smaller, and vice versa. Partitioning of the TP pool between standing stocks of algae and large zooplankton has been suggested as a possible explanation for much of the residual variation in the TP–Chl models (Harris 1980). This hypothesis was tested with data collected on spring TP < 250 µm and average summer TP < 250 µm, Chl *a* (Tables 2 and 16), and contribution of large zooplankton to the TP pool. In 1981, spring and summer were arbitrarily defined as the months of May, and June to August, respectively. Ice melt was very late in 1982. To make the data collected over the two years comparable relative to ice melt, in 1982 spring and summer were defined as 27 May to 17 June, and 18 June to 15 September, respectively. The contribution of large zooplankton to the TP pool was estimated by the percent of TP in PP > 250 µm in 1981 and percent of TP in ZP > 250 µm in 1982 (Table 15). Because ZP > 250 µm was only measured in 1982, separate comparisons were made for data collected in the two years.

The sample sizes (15 in 1981 and 12 in 1982) were too small to use a multiple regression of Chl *a* on TP < 250 µm and PP > 250 µm or ZP > 250 µm. To estimate the contribution of large zooplankton to the residual variation in the TP–Chl models, an approach appropriate for small samples was chosen. Independent TP–Chl models were used to predict ($\log_{10}$) mean summer [Chl *a*] from concentrations of TP < 250 µm measured in either spring or summer. Deviations of the predicted and the observed Chl values were compared with the fraction of the TP pool tied up in PP or ZP > 250 µm. To predict mean summer [Chl *a*] Dillon and Rigler's (1974) model was used with spring TP values measured in 1981:

$$\log_{10}[\text{Chl } a] = -1.136 + 1.448 \log_{10}[\text{TP}]_{sp} \qquad (5)$$

Jones and Bachmann's (1976) model was used with summer TP values measured in 1981:

$$\log_{10}[\text{Chl } a] = -1.09 + 1.46 \log_{10}[\text{TP}]\text{su} \quad (6)$$

models based on data collected from Alberta lakes in 1980 and 1981 were used with both spring and summer TP values in 1982 (Equations 1 and 3, Section 4):

$$\log_{10}[\text{Chl } a] = -0.676 + 1.119 \log_{10}[\text{TP}]\text{sp} \quad (7)$$

and:

$$\log_{10}[\text{Chl } a] = -0.661 + 1.146 \log_{10}[\text{TP}]\text{su} \quad (8)$$

[TP]sp and [TP]su refer to concentrations of TP < 250 μm in spring and summer, respectively. Equations 7 and 8 were not used with the 1981 data because they are based in part on these same data.

In both years, the fraction of TP in the large zooplankton was correlated with the deviations of the predicted [Chl *a*] based on the spring values of TP < 250 μm, from the observed [Chl *a*] (Equations 5 and 7). In 1981, 58% of the variation in the spring TP–summer Chl relationship was accounted for by the relative contribution of PP > 250 μm to the TP pool ($r^2 = 0.58$, $n = 15$, $P < 0.01$; Figure 12). Similarly, in 1982 62% of the variation in the spring TP–summer Chl relationship was accounted for by the relative contribution of ZP > 250 μm to the TP pool ($r^2 = 0.62$, $n = 12$, $P < 0.01$; Figure 13). However, the fraction of TP in the large zooplankton was not correlated with the deviations of the predicted [Chl *a*], based on the summer values (Equations 6 and 8) of TP < 250 μm, from the observed [Chl *a*] ($r^2 = 0.15$, $n = 15$, $P = 0.15$ for 1981; $r^2 = 0.05$, $n = 12$, $P = 0.48$ for 1982). Thus, the fraction of the TP pool in the large zooplankton explained a significant amount of the variation in the spring TP–summer Chl models, but not in the summer TP–summer Chl models.

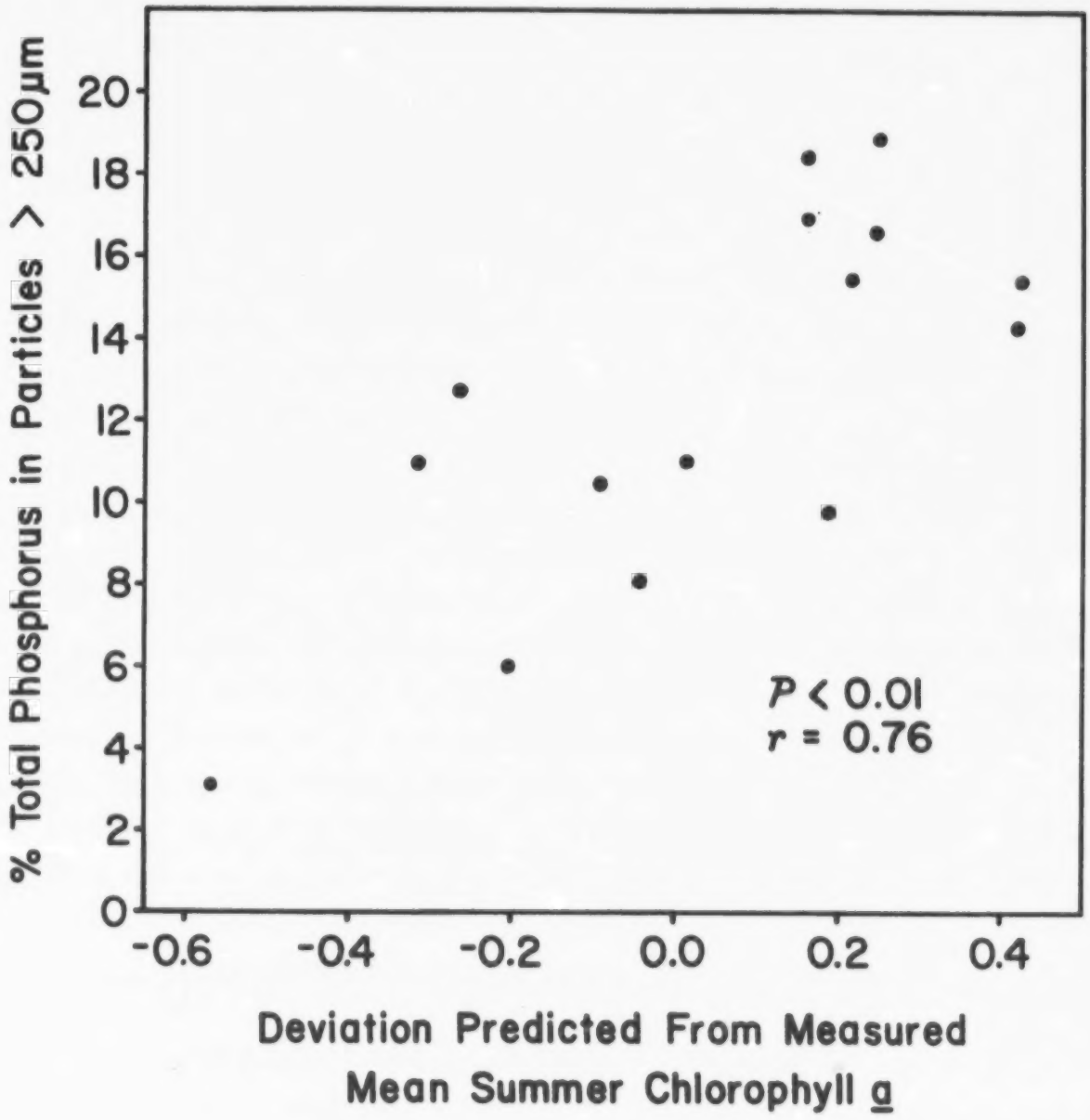

Figure 12. Relationship between percent of the total phosphorus pool in particulate phosphorus (particulates) > 250 µm and the deviations of the predicted concentration of chlorophyll *a* ([Chl *a*]) based on spring concentration of TP < 250 µm and observed [Chl *a*] in 15 lakes in central Alberta in 1981.

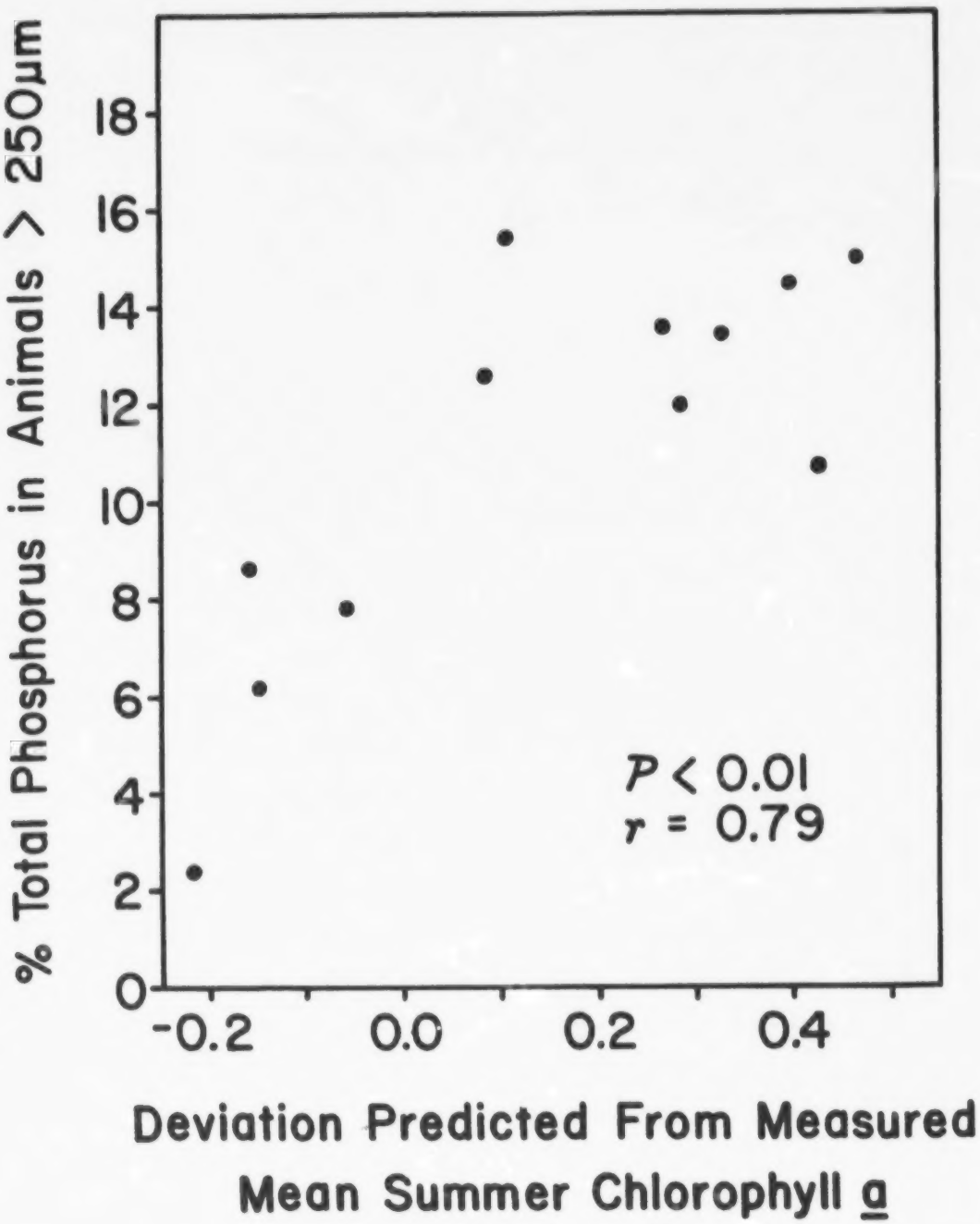

Figure 13. Relationship between percent of the total phosphorus pool in the animal portion of particulate phosphorus (animals) > 250 µm and the deviations of the predicted concentration of chlorophyll *a* ([Chl *a*]) based on spring concentration of TP < 250 µm and observed [Chl *a*] in 12 lakes in central Alberta in 1982.

7.4 DISCUSSION

In this study, PP > 250 µm was an important part of the TP pool in the euphotic zone in summer (avg 13%, Table 15) but decreased to undetectable levels below this zone. Prepas and Rigler (1982) reported similar results for Bob Lake, a lake on the Precambrian Shield. However, contrary to the Bob Lake study, in this study the relative importance of PP > 250 µm varied by as much as seven-fold over a summer in individual lakes. Also, contrary to the previous study, PP > 250 µm tended to aggregate below the epilimnion when the euphotic zone was relatively deep. These results have important implications for sampling programmes designed to collect estimates of PP > 250 µm for an entire lake. (1) To estimate the contribution of large particles to the TP pool, PP > 250 µm should be sampled throughout the study period. (2) Particle phosphorus > 250 µm should be estimated from the euphotic zone, rather than from surface water samples.

In this study, the vertical distribution of PP > 250 µm and Chl *a* were alike in summer (as illustrated in Figure 10). Similarly, the vertical distribution of the zooplankton and phytoplankton biomasses are often alike (Schindler and Noven 1971; Longhurst 1976; Herman et al. 1981). Our results likely apply generally in the study area since the majority of PP > 250 µm was large zooplankton and Chl *a* is an estimate of phytoplankton biomass.

The average summer concentrations of PP > 250 µm and ZP > 250 µm were not correlated with mean summer [Chl *a*]. However, the percentages of the TP pool in PP > 250 µm or ZP > 250 µm were negatively correlated with [Chl *a*]. These results are in agreement with the idea (Harris 1980) that the TP pool is partitioned between the standing stocks of algae and large zooplankton.

There are suggestions that the large zooplankton can regulate the size of the phytoplankton community (Shapiro et al. 1975; Burgi et al. 1979; Lynch and Shapiro 1981; Hoyer and Jones 1983). These observations prompted Harris (1980) to postulate that some of the residual variation in the TP–Chl models is due to the relative size of the zooplankton community. This hypothesis was tested with data collected on the relative contribution of PP > 250 µm during summer to the TP pool. However, the relative size of the large zooplankton community (estimated as PP) did not consistently

account for a significant fraction of the residual variation in the TP–Chl models. The spring TP–summer Chl models were improved by including an estimate of the contribution of large zooplankton to the TP pool in summer, whereas the summer TP–summer Chl models were not improved when the same factor was included.

These conflicting results are probably due to different patterns in open–water levels of TP < 250 μm and PP > 250 μm in shallow and deep lakes in this region. In shallow lakes, levels of TP < 250 μm increase in the euphotic zone during the period from ice–out to late summer whereas in deep lakes, TP < 250 μm decrease (Section 4.2). As a result, summer Chl levels are high in shallow lakes as compared to deep lakes when judged relative to spring TP values (Riley and Prepas, unpublished). In addition, PP > 250 μm and ZP > 250 μm tended to be a smaller portion of the TP pool in shallow as compared with the deep lakes (avg summer values 15 and 10%, Table 15). Thus, the relatively high Chl levels and the low percentage of the TP pool in PP > 250 μm in shallow lakes relative to spring levels of TP < 250 μm, but not summer levels of TP < 250 μm, could account for the conflicting results reported here.

Although the fraction PP > 250 μm is a significant portion of the TP pool, good estimates of this fraction do not improve the TP–Chl relationship in our study lakes. However this fraction is important when considering seasonal variation in the TP pool (e.g., Prepas and Rigler 1981).

8. SUMMARY OF THE INFLUENCE OF PHOSPHORUS AND ZOOPLANKTON ON CHLOROPHYLL LEVELS IN ALBERTA LAKES

1. Total phosphorus (TP) was a reasonable predictor of lake greeness or mean summer [Chl *a*] for freshwater lakes in Alberta.
2. Summer [TP] was a better predictor than spring [TP] of mean summer [Chl *a*] for Alberta lakes due to large temporal fluctuations in [TP].
3. The temporal fluctuations in [TP] were different in Alberta lakes which mixed intermittently throughout summer (i.e., shallow lakes) than in Alberta lakes which remained permanently thermally stratified during this period (i.e., deep lakes). In the shallow lakes, [TP] tended to increase during summer, whereas in deep lakes [TP] decreased.
4. In shallow Alberta lakes, [TP] increased in the water over the sediments when the water was thermally stratified. Later, during mixing, some of this phosphorus was incorporated into the surface waters. In summer, [TP] increased sporadically in most shallow lakes.
5. In deep Alberta lakes, [TP] also increased in the water over the sediments during summer. Some of this TP was mixed into the surface waters only when both the thermocline was depressed and the concentration of dissolved phosphorus in the top of the hypolimnion was relatively high. Over most of the summer, the [TP] decreased or remained constant in deep lakes.
6. The release of phosphorus from lake sediments was associated with low levels of dissolved oxygen in the water over the sediments. In deep lakes,the rate of phosphorus release from lake sediments was related to lake productivity.
7. Temporal fluctuations in [TP] were paralleled by fluctuations in [Chl *a*] in summer in Alberta lakes.
8. A significant but variable portion of the TP pool in Alberta lakes was tied up in large zooplankton.
9. The fraction of the TP pool tied up in large zooplankton explains a substantial amount of the residual variation in the spring TP–summer Chl *a* model but not the summer TP–summer Chl *a* model for Alberta lakes. These apparently

contradictory results can be explained by differences in shallow and deep lakes.

10. Further study is needed on the effect of high salinity on chlorophyll levels, and on the importance of lake sediments as a source of total phosphorus in Alberta lakes. To evaluate the relative importance of lake sediments in phosphorus budgets, further study is also needed on terrestrial loading and the influence of groundwater in Alberta lakes.

9. REFERENCES CITED

Allan, R.J. and B.C. Kenney. 1978. Rehabilitation of eutrophic prairie lakes in Canada. Internationale Verheiningung fur Theoretische und Angewandte Limnologie 20:214-224.

Bergmann, M. and R.H. Peters. 1980. A simple reflectance method for the measurement of particulate pigment in lakewater and its application to phosphorus-chlorophyll-seston relationships. Canadian Journal of Fisheries and Aquatic Sciences 37:111-114.

Bloesch, J. 1974. Sedimentation und Phosphorhaushalt im Vierwaldstattersee (Horwer Bucht) und im Rotsee. Schweizerische Zeitschrift fur Hydrologie 36:71-186.

Bloesch, J., P. Stadelmann, and H. Buhrer. 1977. Primary production, mineralization, and sedimentation in the euphotic zone of two Swiss lakes. Limnology and Oceanography 22:511-526.

Burgi, H.R. et al. 1979. Der einfluss experimentell variierter zooplanktondichte auf die produktion und sedimentation im hocheutrophen see. Schweizerische Zeitschrift fur Hydrologie 41:38-63.

Carpenter, J.H. 1965. The Chesapeake Bay Institute technique for the Winkler dissolved oxygen method. Limnology and Oceanography 10:141-143.

Chapra, S.C. and S.J. Tarapchak. 1976. A chlorophyll *a* model and its relationship to phosphorus loading plots for lakes. Water Resources Research 12:1260-1264.

Cullen, J.J. 1982. The deep chlorophyll maximum: comparing vertical profiles of chlorophyll *a*. Canadian Journal of Fisheries and Aquatic Sciences 39:791-803.

D'Elia, C.F., P. A. Steudler, and N. Corwin. 1977. Determination of total nitrogen in aqueous samples using persulfate digestion. Limnology and Oceanography 22:760-764.

Dillon, P.J. and F.H. Rigler. 1974a. The phosphorus-chlorophyll relationship in lakes. Limnology and Oceanography 19:767-773.

Dillon, P.J. and F.H. Rigler. 1974b. A test of a simple nutrient budget model predicting the phosphorus concentration in lake water. Journal of the Fisheries Research Board of Canada 31:1771-1778.

Dillon, P.J. and F.H. Rigler. 1975. A simple method for predicting the capacity of a lake for development based on lake trophic status. Journal of the Fisheries Research Board of Canada 31:1519-1531.

Environment Canada. Inland Water Directorate. Water Quality Branch. 1979. Analytical methods manual. Ottawa, Canada.

Fee, E.J. 1976. The vertical and seasonal distribution of chlorophyll in lakes of the Experimental Lakes Area, northwestern Ontario: Implications for primary production estimates. Limnology and Oceanography 21:767-783.

Gallup, D.N. 1978. Lakes of central Alberta with emphasis upon Moose Lake. International Vereinigung fur Theoretische und Angewandte Limnologie 26:182-189.

Hanson, J.M. and W.C. Leggett. 1982. Empirical prediction of fish biomass and yield. Canadian Journal of Fisheries and Aquatic Sciences 39:257-263.

Harris, G.P. 1980. Temporal and spatial scales in phytoplankton ecology. Mechanisms, methods, models, and management. Canadian Journal of Fisheries and Aquatic Sciences 37:877-900.

Hartmann, J. and W. Numann. 1977. Percids of Lake Constance, a lake undergoing eutrophication. Journal of the Fisheries Research Board of Canada 34:1670-1677.

Herman, A.W., D.D. Sameoto, and A.R. Longhurst. 1981. Vertical and horizontal distribution patterns of copepods near the shelf break south of Nova Scotia. Canadian Journal of Fisheries and Aquatic Sciences 38:1065-1076.

Hickman, M. 1980. Phosphorus, chlorophyll and eutrophic lakes. Archiv fur Hydrobiologie 88:137-145.

Holdren, G.C. and D.E. Armstrong. 1980. Factors affecting phosphorus release from intact lake sediment cores. Environmental Science and Technology 14:79-87.

Holm-Hansen, O. et al. 1965. Fluorometric determinations of chlorophyll. Journal du Conseil, Conseil International pour l'Exploration de la Mer 30:3-15.

Hoyer, M.V. and J.R. Jones. 1983. Factors affecting the relationship between phosphorus and chlorophyll *a* in midwestern reservoirs. Canadian Journal of Fisheries and Aquatic Sciences 40:192-199.

Hutchinson, G.E. 1957. A treatise on limnology: I. New York, N.Y: Wiley, 1015 pp.

Jones, J.R. and R.W. Bachmann. 1976. Prediction of phosphorus and chlorophyll levels in lakes. Journal of Water Pollution Federation 48:2176-2182.

Larsen, D.P. et al. 1975. Response of eutrophic Shagawa Lake, Minnesota, U.S.A., to point-source, phosphorus reduction. Internationale Vereinigung fur Theoretische und Angewandte Limnologie 19:884-892.

Larsen, D.P., D.W. Schults, and K.W. Malueg. 1981. Summer internal phosphorus supplies in Shagawa Lake, Minnesota. Limnology and Oceanography 26:740-753.

Longhurst, A.R. 1976. Interactions between zooplankton and phytoplankton profiles in the eastern tropical Pacific Ocean. Deep-Sea Research 23:729-754.

Lynch, M. and J. Shapiro. 1981. Predation, enrichment, and phytoplankton community structure. Limnology and Oceanography 26:86-102.

Matuszek, J.E. 1978. Empirical predictions of fish yields of large North American lakes. Transactions of the American Fisheries Society 107:385-394.

McCauley, E. and J. Kalff. 1981. Empirical relationships between phytoplankton and zooplankton biomass in lakes. Canadian Journal of Fisheries and Aquatic Sciences 38:458-463.

Menzel, D.W. and N. Corwin. 1965. The measurement of total phosphorus in seawater based on the liberation of organically bound fractions by persulfate oxidation. Limnology and Oceanography 10:280-282.

Morris, J.E. and W. Stumm. 1967. Redox equilibria and measurements of potentials in the aquatic environment. *In* Equilibrium concepts in natural systems, ed. R.F. Gould. Washington, D.C.: American Chemical Society, pp. 270-285.

Nicholls, K.H. and P.J. Dillon. 1978. An evaluation of phosphorus-chlorophyll-phytoplankton relationships for lakes. International Revue Gesamten Hydrobiologie 63:141-154.

Oglesby, R.T. 1977. Relationships of fish yield to lake phytoplankton standing crop, production, and morphoedaphic factors. Journal of the Fisheries Research Board of Canada 34:2271-279.

Olsen, S. 1958. Phosphate adsorption and isotopic exchange in lake muds. Internationale Vereiningung fur Theoretische und Angewandte Limnologie 13:915-922.

Prepas, E. and F.H. Rigler. 1978. The enigma of *Daphnia* death rates. Limnology and Oceanography 23: 970-988.

Prepas, E.E. and F.H. Rigler. 1981. A test of a simple model to predict short-term changes in the phosphorus concentration in lake water. Internationale Vereinigung fur Theoretische und Angewandte Limnologie 21:187-196.

Prepas, E.E. and F.H. Rigler. 1982. Improvements in quantifying the phosphorus concentration in lake water. Canadian Journal of Fisheries and Aquatic Sciences 39:822-829.

Rawson, D.S. 1951. The total mineral content of lake waters. Ecology 32:669-672.

Rawson, D.S. and J.E. Moore. 1944. The saline lakes of Saskatchewan. Canadian Journal of Research, D. 22:141-201.

Ryder, R.A. 1965. A method for estimating the potential fish production of north-temperate lakes. Transactions of the American Fisheries Society 94:214-218.

Ryder, R.A. 1982. The morphoedaphic index - use, abuse, and fundamental concepts. Transactions of the American Fisheries Society 111:154-164.

Ryder, R.A. et al. 1974. The morphoedaphic index, a fish yield estimator-review and evaluation. Journal of the Fisheries Research Board of Canada 31:663-688.

Sakamoto, M. 1966. Primary production by phytoplankton community in some Japanese lakes and its dependence on lake depth. Archiv fur Hydrobiologie 62:1-28.

Schindler, D.W. 1977. Evolution of phosphorus limitation in lakes. Science 195:260-262.

Schindler, D.W. and E.J. Fee. 1974. Experimental Lakes Area: whole-lake experiments in eutrophication. Journal of the Fisheries Research Board of Canada 31:937-953.

Schindler, D.W. and B. Noven. 1971. Vertical distribution and seasonal abundance of zooplankton in two shallow lakes of the experimental lakes area northwestern Canada. Journal of the Fisheries Research Board of Canada 28:245-263.

Schindler, D.W. et al. 1971. Eutrophication of lake 227, Experimental Lakes Area, northwestern Ontario, by addition of phosphate and nitrate. Journal of the Fisheries Research Board of Canada 28:1763-1782.

Schindler, D.W. et al. 1973. Eutrophication of lake 227 by addition of phosphate and nitrate: the second, third, and fourth years of enrichment, 1970, 1971, and 1972. Journal of the Fisheries Research Board of Canada 30:1415-1440.

Shapiro, J., V. Lamarra, and M. Lynch. 1975. Biomanipulation: an ecosystem approach to lake restoration, pp. 85-96. In Proceedings of the Symposium on Water Quality Management Through Biological Control, ed. P.L. Brezanik and J.L. Fox. Gainesville, Florida. January 23-30, 1975; University of Florida, p 164.

Smith, P.E., R.C. Counts, and R.I. Clutter. 1968. Changes in filtering efficiency of plankton nets due to clogging under tow. Journal du Conseil, Conseil International pour l'Exploration de la Mer 32:232-248.

Smith, V.H. 1979. Nutrient dependence of primary productivity in lakes. Limnology and Oceanography 24:1051-1064.

Smith, V.H. 1982. The nitrogen and phosphorus dependence of algal biomass in lakes: an empirical and theoretical analysis. Limnology and Oceanography 27:1101-1112.

Snedecor, G.W. and W.G. Cochran. 1980. Statistical methods, 7th ed. Ames, Iowa: Iowa State University. 507 pp.

Sokal, R.R. and F.J. Rohlf. 1981. Biometry, 2nd ed. San Francisco: Freeman. 859 pp.

Solorzano, L. 1969. Determination of ammonia in natural waters by phenolhypochlorite method. Limnology and Oceanography 14:799-801.

Stainton, M.P., M.J. Capel, and F.A.J. Armstrong. 1977. The chemical analysis of freshwater, 2nd ed. Fisheries and Environment Canada, Miscellaneous Special Publication 25. (Available from the Freshwater Institute, Winnipeg, Man.) Ottawa. 180 pp.

Stefan, H.G. and M.J. Hanson. 1981. Phosphorus recycling in five shallow lakes. Journal of the Environmental Engineering Division, ASCE 107:713-730.

Stewart, K.M. and S.J. Markello. 1974. Seasonal variations in concentrations of nitrate and total phosphorus, and calculated nutrient loading for six lakes in western New York. Hydrobiologia 44:61-89.

Vollenweider, R.A. 1976. Rotsee, a source, not a sink for phosphorus? A comment to and a plea for nutrient balance studies. Hydrologie 38:29-34.

Wagner, G. 1967. Beitrage zum sauerstoff-, stickstoff- und phosphorhaushalt des Bodensees. Archiv fur Hydrobiologie 63:86-103.

Willemsen, J. 1977. Population dynamics of percids in Lake Ijssel and some smaller lakes in the Netherlands. Journal of the Fisheries Research Board of Canada 34:1710-1719.

Yentsch, C.S. and D.W. Menzel. 1963. A method for the determination of phytoplankton chlorophyll and phaeophytin by fluorescence. Deep-Sea Research 10:221-231.

10. APPENDIX

Temperature, chlorophyll, total nitrogen, and total phosphorus data collected in 1982 for 12 lakes in central Alberta and species lists for zooplankton in the lakes studied in 1981 and 1982.

Table 17. Temperature profiles (°C) for Amisk N. Lake, 1982.

	Date						
Depth	5/17	6/7	6/28	7/19	8/9	8/31	9/20
0	8.1	14.6	21.3	20.6	20.5	14.6	13.3
1	7.8	13.5	20.3	20.6	20.4	14.6	13.3
2	7.6	12.0	19.8	20.5	20.4	14.6	13.3
3	6.8	11.4	19.2	20.5	20.1	14.6	13.3
4	6.6	10.9	17.6	19.3	18.2	14.6	13.3
5	6.3	10.8	13.9	17.7	18.2	14.6	13.2
6	6.1	10.3	11.7	14.6	18.2	14.6	13.2
7	5.9	10.0	10.6	12.1	12.8	14.5	13.2
8	5.8	9.8	9.6	10.3	11.1	13.4	12.6
9	5.6	8.6	8.9	9.5	7.7	10.4	12.3
10	4.9	7.8	8.1	7.3	7.2	8.8	11.2
11	4.8	7.2	7.3	7.2	6.8	8.1	9.3
12	4.7	6.7	7.0	6.7	6.8	7.5	7.8
13	4.7	6.3	6.6	6.4	*6.7	7.1	7.5
14	4.7	5.8	6.4	6.1	*6.4	6.8	7.2
15	4.5	5.6	6.1	6.0	*6.3	6.6	7.0
16	4.4	5.5	6.0	5.9	*6.2	6.5	6.8
17	4.3	5.4	5.9	5.7	*6.1	6.4	6.6
18	4.3	5.2	5.8	5.7	*6.0	6.3	6.6
19	4.2	5.2	5.8	5.7	*6.0	6.2	6.5
20	4.2	5.1	5.7	5.7	*5.9	6.2	6.5
21	4.1	5.1	5.7	5.7	*5.9	6.2	6.4
22	4.1	5.1	5.6	5.6	*5.9	6.2	6.4
23	4.1	5.1	5.6	5.5	*5.8	6.1	6.4
24	4.1	5.0	5.6	5.4	*5.8	6.1	6.3
25	4.1	5.0	5.6	5.4	*5.7	6.0	6.3
26	4.0	5.0	5.5	5.4	*5.7	6.0	6.3
27	4.0	5.0	5.5	5.4	*5.7	6.0	6.3
28	4.0	5.0	5.4	5.4	*5.7	6.0	6.3
29	4.0	5.0	5.4	5.4	*5.7	6.0	6.3
30	4.0	5.0	5.4	5.4	*5.7	6.0	6.3

* Interpolated values.

Table 18. Temperature profiles (°C) for Amisk S. Lake, 1982.

Depth	Date						
	5/17	6/7	6/28	7/19	8/9	8/31	9/20
0	7.7	15.5	20.7	20.0	18.4	14.7	12.9
1	6.8	14.4	20.4	20.0	18.2	14.7	12.8
2	6.1	13.1	20.0	19.8	18.1	14.7	12.8
3	5.9	12.9	19.5	19.6	18.0	14.6	12.8
4	5.6	12.5	16.0	19.4	18.0	14.6	12.7
5	5.6	12.3	13.8	16.5	16.0	14.6	12.7
6	5.4	12.1	12.1	13.4	15.5	14.6	12.6
7	5.2	11.8	11.2	10.9	12.0	14.5	12.4
8	5.1	11.0	9.7	9.6	10.4	10.8	12.3
9	5.0	8.1	8.9	8.7	7.9	9.1	11.9
10	5.0	7.3	8.3	8.0	7.4	8.3	10.8
11	4.8	6.9	7.5	7.6	7.1	7.9	9.7
12	4.4	6.7	6.9	7.2	6.8	7.6	8.3
13	4.2	6.5	6.7	6.8	6.7	7.4	7.8
14	4.2	6.5	6.5	6.6	6.4	7.1	7.4
15	4.1	6.2	6.2	6.2	6.2	6.9	6.8
16	4.1	5.9	5.9	6.0	6.1	6.6	6.6
17	4.1	5.7	5.6	5.8	5.8	6.2	6.4
18	4.0	5.1	5.4	5.5	5.6	5.8	6.2
19	4.0	4.6	5.1	5.1	5.4	5.4	5.8
20	3.8	4.4	4.8	4.9	5.2	5.2	5.6
21	3.8	4.3	4.7	4.7	5.0	4.9	5.3
22	3.8	4.2	4.7	4.4	*4.8	4.8	5.1
23	3.8	4.1	4.6	4.4	*4.6	4.6	5.0
24	3.7	4.1	4.5	4.3	*4.4	4.5	4.9
25	3.7	4.1	4.4	4.2	*4.3	4.4	4.7
26	3.7	4.0	4.3	4.2	*4.3	4.4	4.7
27	3.7	4.0	4.2	4.2	*4.2	4.3	4.6
28	3.7	4.0	4.1	4.1	*4.2	4.2	4.6
29	3.7	4.0	4.1	4.0	*4.1	4.2	4.5
30	3.7	3.9	4.0	4.0	*4.1	4.1	4.4
31	3.7	3.8	4.0	3.8	*4.0	4.0	4.3
32	3.6	3.8	4.0	3.8	*4.0	4.0	4.3
33	3.6	3.8	4.0	3.7	*3.9	4.0	4.3
34	3.6	3.7	3.9	3.7	*3.9	4.0	4.3
35	3.6	3.7	3.9	3.7	*3.9	3.9	4.2
36	3.6	3.7	3.9	3.7	*3.9	3.9	4.2
37	3.6	3.7	3.8	3.7	*3.9	3.9	4.2
38	3.6	3.7	3.8	3.6	*3.8	3.9	4.2
39	3.4	3.7	3.8	3.6	*3.8	3.9	4.1
40	3.4	3.7	3.8	3.6	*3.8	3.8	4.1
41	3.4	3.7	3.8	3.6	*3.8	3.8	4.1
42	3.4	3.7	3.8	3.6	*3.8	3.8	4.1
43	3.4	3.7	3.8	3.6	*3.7	3.8	4.1
44	3.4	3.7	3.7	3.6	*3.7	3.8	4.1
45	3.3	3.6	3.7	3.6	*3.7	3.8	4.1
46	3.3	3.6	3.7	3.6	*3.7	3.8	4.1
47	3.3	3.6	3.7	3.6	*3.7	3.8	4.0
48	3.2	3.6	3.7	3.6	*3.7	*3.8	4.0
49	3.2	3.6	3.7	3.6	*3.7	*3.8	4.0
50	3.2	3.6	3.7	3.6	*3.7	*3.8	4.0

* Interpolated values.

Table 19. Temperature profiles (°C) for Baptiste N. Lake, 1982.

	Date						
Depth	5/18	6/7	6/29	7/20	8/10	9/1	9/21
0	7.8	13.2	17.8	19.5	18.2	14.9	14.6
1	7.7	13.0	17.8	19.2	18.2	14.8	13.6
2	7.5	13.0	17.8	19.0	18.1	14.8	13.3
3	7.3	12.9	16.8	18.9	18.0	14.8	13.3
4	7.2	12.9	16.1	18.8	17.7	14.7	13.2
5	7.1	12.9	14.3	18.7	15.1	14.7	13.2
6	6.9	12.8	13.6	15.9	14.9	14.7	13.2
7	6.2	11.4	12.1	13.0	14.0	14.6	13.2
8	5.7	11.0	11.0	11.6	13.5	14.6	13.0
9	5.3	9.8	10.7	11.2	12.3	14.6	13.0
10	5.1	*9.4	10.6	10.7	11.2	14.6	13.0
11	4.9	*9.2	10.4	10.6	10.8	11.5	13.0
12	4.8	*9.0	10.2	10.5	10.5	11.1	12.9

*Interpolated values.

Table 20. Temperature profiles (°C) for Baptiste S. Lake, 1982.

Depth	Date						
	5/18	6/8	6/29	7/20	8/10	9/1	9/21
0	7.3	13.6	18.0	18.8	18.6	14.7	13.9
1	7.2	13.6	18.0	18.8	18.6	14.7	13.7
2	7.1	13.6	18.0	18.7	18.5	14.7	13.7
3	6.8	13.6	17.8	18.6	18.4	14.7	13.6
4	6.7	13.6	16.5	18.6	18.3	14.7	13.6
5	6.2	12.5	14.8	18.0	17.6	14.7	13.6
6	5.8	10.4	12.1	17.0	16.5	14.7	13.5
7	5.4	9.2	10.9	13.5	14.3	14.6	13.0
8	5.2	8.3	9.2	9.9	12.4	14.6	12.8
9	5.2	7.7	8.3	8.8	9.5	10.2	12.3
10	5.1	7.3	7.3	8.2	8.3	8.5	11.2
11	4.9	7.0	7.0	7.3	7.6	7.8	9.2
12	4.8	6.7	6.6	6.6	6.8	7.0	7.5
13	4.7	6.2	6.2	6.3	6.4	6.6	7.0
14	4.7	6.0	6.0	6.1	6.2	6.3	6.7
15	4.5	5.9	5.9	6.0	6.0	6.1	6.4
16	4.4	5.8	5.8	5.8	5.8	5.9	6.2
17	4.3	5.7	5.6	5.5	5.6	5.8	6.0
18	4.0	5.7	5.6	5.4	5.5	5.6	5.8
19	3.8	5.6	5.5	5.3	5.4	5.6	5.8
20	3.8	5.5	5.4	5.3	5.4	5.6	5.8
21	3.8	5.4	5.4	5.3	5.4	5.6	5.7
22	3.6	5.4	5.3	5.3	5.4	5.5	5.7
23	3.6	5.4	5.3	5.3	5.4	5.5	5.7

Table 21. Temperature profiles (°C) for Eden Lake, 1982.

	Date						
Depth	5/12	6/1	6/22	7/13	8/4	8/23	9/14
0	9.4	16.4	22.4	22.3	19.8	18.8	13.7
1	9.3	16.0	22.4	21.9	19.4	18.8	13.7
2	9.2	15.3	22.3	21.1	19.3	18.7	13.7
3	7.0	14.4	19.9	19.3	19.1	18.5	13.7
4	5.0	10.7	14.3	17.5	19.1	18.2	13.6
5	4.6	6.2	9.4	12.8	14.3	15.5	13.5
6	4.3	5.3	6.8	8.6	10.0	11.6	12.6
7	4.2	4.9	5.7	6.7	7.7	8.9	9.0
8	4.1	4.6	5.1	6.1	6.4	7.7	7.1
9	4.1	4.5	4.8	5.5	5.6	6.8	6.2
10	4.0	4.5	4.7	5.3	5.3	6.7	5.8
11	4.0	4.5	4.7	5.1	5.1	6.6	*5.7
12	4.0	4.4	4.7	5.0	5.0	6.5	*5.6

* Interpolated values.

Table 22. Temperature profiles (°C) for Hasse Lake, 1982.

Depth	Date							
	5/11	5/31	6/15	7/6	7/27	8/17	9/7	9/27
0	7.7	14.6	20.8	17.4	21.0	18.3	15.3	13.2
1	7.2	14.5	20.8	17.3	20.9	18.3	15.2	13.2
2	6.6	14.4	20.0	17.2	20.2	18.3	15.2	13.2
3	6.1	14.2	16.5	17.2	19.3	18.2	15.1	13.2
4	5.7	13.4	14.8	17.1	18.7	18.2	14.8	13.2
5	5.5	12.7	13.6	16.6	17.8	18.1	14.7	13.2
6	5.4	10.6	11.6	13.1	14.5	16.7	14.6	13.2
7	5.3	8.5	10.4	10.5	11.6	12.3	14.0	13.2
8	4.6	7.9	*9.1	9.2	10.0	10.2	11.0	13.2
9	*4.4	7.4	*7.9	8.3	9.2	9.9	10.2	13.2

* Interpolated values.

Table 23. Temperature profiles (°C) for Lessard Lake, 1982.

	Date						
Depth	5/25	6/9	6/21	7/12	8/3	8/24	9/13
0	13.1	15.4	22.1	20.5	18.4	17.8	13.2
1	13.1	14.8	22.1	20.5	18.4	17.8	13.1
2	13.1	14.6	22.0	20.4	18.4	17.8	13.1
3	13.1	14.5	19.3	17.2	18.4	17.8	13.1
4	13.1	14.3	15.6	16.7	18.4	17.8	13.1
5	13.1	14.0	14.6	16.5	18.4	17.8	13.1

Table 24. Temperature profiles (°C) for Mink Lake, 1982.

Depth	Date						
	5/11	5/31	6/15	7/6	7/27	8/17	9/7
0	6.0	15.0	20.1	17.9	22.2	19.4	16.2
1	5.9	14.7	20.0	17.6	21.7	19.0	15.9
2	5.6	14.6	19.8	17.5	20.5	18.3	15.7
3	5.0	13.2	17.4	17.5	19.1	18.2	15.5
4	4.8	12.8	16.2	17.4	18.7	18.2	15.4
5	4.7	12.7	15.2	17.3	18.4	18.2	15.2
6	4.6	12.4	14.3	17.0	17.0	17.8	15.2
7	4.4	12.2	13.4	15.8	15.7	17.6	15.1
8	4.3	12.0	12.5	13.7	*14.4	*17.5	*15.0

* Interpolated values

Table 25. Temperature profiles (°C) for Peanut Lake, 1982.

	Date						
Depth	5/25	6/9	6/21	7/12	8/3	8/24	9/13
0	15.3	16.7	23.4	22.6	19.6	19.1	14.5
1	15.3	16.6	22.8	22.2	19.6	19.0	14.4
2	15.2	16.3	21.8	21.8	19.6	18.9	14.4
3	15.2	16.2	19.0	21.1	19.6	18.9	14.3
4	9.4	14.0	16.0	18.2	19.6	18.8	14.2
5	7.1	10.0	12.1	13.6	16.5	17.2	14.2
6	6.2	7.4	9.6	11.4	12.7	14.6	14.2
7	5.8	6.6	8.3	9.6	10.1	11.2	13.5
8	5.6	6.2	7.3	7.1	8.2	9.1	9.5
9	5.4	5.9	6.6	6.8	7.3	7.8	7.9
10	5.4	5.8	6.2	6.6	6.9	7.3	7.4
11	5.4	5.6	6.0	6.4	6.7	7.2	7.2
12	5.3	5.6	6.0	6.4	6.7	7.1	7.0

Table 26. Temperature profiles (°C) for Sauer Lake, 1982.

	Date						
Depth	5/12	6/1	6/22	7/13	8/4	8/23	9/14
0	10.7	16.3	23.2	21.9	19.5	17.8	13.6
1	10.7	16.3	23.0	21.8	19.5	17.8	13.6
2	8.3	15.3	22.6	21.2	19.4	17.8	13.6
3	6.3	13.7	18.4	19.3	19.3	17.5	13.6
4	5.3	8.6	13.6	16.9	18.8	16.8	13.6
5	5.0	6.4	9.2	11.9	13.9	14.6	13.5
6	4.9	5.3	6.4	8.7	10.6	11.9	13.1
7	4.5	4.9	5.7	6.5	7.5	8.2	9.5
8	4.4	4.8	5.3	5.8	6.2	6.7	7.3
9	4.4	4.7	5.2	5.4	5.4	5.9	6.1
10	4.4	4.6	5.0	5.1	5.0	5.2	5.4
11	4.4	4.6	5.0	5.0	4.9	5.2	5.2
12	4.4	4.6	4.9	5.0	4.8	5.1	5.0
13	4.4	4.6	4.9	4.9	4.8	5.0	4.9

Table 27. Temperature profiles (°C) for Twin Lake, 1982.

Depth	Date					
	5/26	6/14	7/5	7/26	8/18	9/8
0	10.8	18.4	13.7	17.4	17.6	14.7
1	10.7	18.4	13.7	17.2	17.4	14.6
2	10.7	16.3	13.7	16.5	17.1	14.6
3	10.6	14.4	13.7	15.2	16.8	13.8
4	10.2	12.7	13.0	13.8	16.0	13.6
5	8.4	10.5	11.7	11.3	12.2	13.0
6	7.3	8.5	11.3	9.9	10.2	10.3
7	5.9	7.2	9.0	8.6	8.2	8.6
8	5.0	6.3	6.7	6.7	6.9	6.8
9	4.7	5.2	5.7	5.1	5.9	6.0
10	4.4	4.6	5.1	4.5	5.3	5.4
11	4.2	4.4	4.7	4.1	5.0	5.0
12	4.1	4.2	4.4	4.0	4.6	4.6
13	4.0	4.1	4.3	3.9	4.4	4.2
14	3.9	4.0	4.1	3.8	4.2	4.0
15	3.8	3.9	4.0	3.8	4.1	3.8
16	3.7	3.8	3.9	3.7	4.0	3.8
17	3.7	3.8	3.9	3.7	4.0	3.8
18	3.7	3.7	3.8	3.6	3.9	3.8
19	3.6	3.7	3.8	3.6	3.9	3.8
20	3.6	3.7	3.8	3.6	3.8	3.8
21	3.6	3.7	3.7	3.6	3.8	3.8
22	3.6	3.7	3.7	3.6	3.8	3.8
23	3.6	3.7	3.7	3.6	3.8	3.8
24	3.6	3.7	3.7	3.6	3.8	3.7
25	3.6	3.7	3.7	3.6	3.8	3.7
26	3.6	3.7	3.7	3.6	3.8	3.7
27	3.6	3.6	3.7	3.6	3.8	3.7
28	3.6	3.6	3.7	3.6	3.8	3.7
29	3.6	3.6	3.7	3.6	3.8	3.7
30	3.6	3.6	3.7	3.6	3.8	3.7

Table 28. Temperature profiles (°C) for Wizard Lake, 1982.

Depth	Date						
	5/26	6/14	7/5	7/26	8/18	9/8	9/27
0	12.3	20.4	16.9	20.4	21.2	17.2	13.6
1	12.3	19.3	16.9	19.5	19.9	17.0	13.6
2	12.3	18.2	16.9	18.8	19.2	16.8	13.6
3	12.3	16.0	16.8	18.6	18.9	16.7	13.6
4	12.1	14.3	16.8	17.8	18.7	16.4	13.6
5	11.8	13.7	16.7	17.6	18.6	16.1	13.6
6	11.5	13.1	16.7	17.5	18.4	15.9	13.6
7	11.3	12.2	16.4	16.8	18.2	15.7	13.6
8	11.0	11.5	15.6	15.3	17.1	15.6	13.6
9	10.1	10.8	12.1	14.0	16.1	15.6	13.6
10	8.6	9.8	10.8	13.2	14.6	15.6	13.6
11	8.0	*9.2	10.0	12.1	13.2	15.2	13.5

* Interpolated values.

Table 29. Vertical profiles of total phosphorus (mg/m³) at Amisk N. Lake, 1982.

	Date						
Depth	5/17	6/7	6/28	7/19	8/9	8/31	9/20
0–2	74.1						
0–4		58.0	42.3		35.7		41.2
0–5	77.1			32.2			
0–7		57.4	46.7			27.9	39.2
10		70.4	91.8	118.4	133.9	126.3	67.0
12		72.5	93.9	121.2	136.5	143.5	143.5
14		79.6	105.5	122.1	148.6	149.0	160.9
16		86.9	107.8	130.5	150.9	158.2	181.1
18		89.5	112.2	128.3	156.5	172.6	187.4
20		91.4	122.1	131.9	161.6	178.5	192.2
22		90.9	127.1	127.3	162.5	179.0	205.0
24		91.9	134.8	126.7	162.9	181.5	206.4
26		97.6	137.2	131.3	164.6	184.0	213.3
28		93.2	131.0	132.6	168.5	190.7	
30		99.3	125.6		175.4	190.3	246.8

Table 30. Vertical profiles of total phosphorus (mg/m³) at Amisk S. Lake, 1982.

	Date						
Depth	5/17	6/7	6/28	7/19	8/9	8/31	9/20
0-4		54.9	44.4		37.7		
0-5				29.4			39.7
0-6	84.3		42.5				
0-7		55.0				29.3	
0-9							41.1
7			57.3	60.1	33.2	26.1	38.0
8		61.4					
9			71.4	90.1	109.7	94.4	45.1
10		74.1					
11			79.7	98.0	119.5	126.2	93.0
12		75.7					
13			80.0	110.6	133.4	134.6	139.4
14		76.9					
15			86.0	102.3	128.2	140.8	139.0
16		79.1					
17			89.8	97.7	122.1	131.1	140.0
18		87.2					
19			108.3	96.9	125.9	131.7	140.4
20		89.5					
21			113.9	107.3	120.5	127.2	143.1
24		95.4					
23			122.5	110.7	129.1	131.7	145.8
24		99.1					
25			127.0	112.4	131.5	135.3	149.4
26		101.3					
27			118.5	120.1	132.1	131.6	153.9
28		107.8					
29			130.0	121.9	139.6	135.7	154.7
30		104.5					
31			134.9	129.5	139.1	143.2	153.4
32		106.5					
33			135.4	131.3	145.3	154.4	158.3
34		107.4					
35			134.2	134.9	148.9	156.3	162.5
36		116.5					
37			130.2	134.0	152.6	161.6	166.5
38		118.9					
39			139.5	132.6	157.9	162.2	172.6
40		119.2					
41			143.4	136.7	165.2	176.4	
42		121.2					
43			143.2	135.6	164.9	178.3	
44		124.6					
45			150.6	146.7	170.9	184.0	
47			153.4	149.5	171.2	188.3	
48		128.7					
49			151.5	168.6	184.4	189.7	

Table 31. Vertical profiles of total phosphorus (mg/m³) at Baptiste N. Lake, 1982.

	Date						
Depth	5/18	6/8	6/29	7/20	8/10	9/1	9/21
0–3	109.0				62.1		
0–4			48.2	55.8		89.1	83.9
0–6		47.8	57.7	57.2			

Table 32. Vertical profiles of total phosphorus (mg/m³) at Baptiste S. Lake, 1982.

	Date						
Depth	5/18	6/8	6/29	7/2	8/10	9/1	9/21
0-2	117.3						
0-3.5					37.1		
0-4	119.3	53.9	49.1				
0-5					35.6	29.9	
0-6		53.0	58.4	30.5			42.1
0-8						28.5	
7		57.6		50.4	56.1	29.9	29.5
9		74.9	57.1	97.7	116.6	160.2	47.9
11		89.2	113.4	142.6	150.5	224.1	185.4
13		112.6	152.8	161.3	213.6	227.8	245.7
15		123.0	167.8	194.9	227.4	289.5	310.9
17		124.8	172.0	243.3	259.7	344.7	383.5
19		135.2	180.7	264.3	295.5	372.6	437.8
21		140.3	204.7	278.4	345.6	397.1	481.1
22		141.5	216.5				
23		148.4		288.4	354.0	476.7	514.2

Table 33. Vertical profiles of total phosphorus (mg/m³) at Eden Lake, 1982.

	Date						
Depth	5/12	6/1	6/22	7/13	8/4	8/23	9/14
0-2	36.8						
0-4		18.5	17.4	16.0	17.2	16.0	
0-5							15.2
0-6	43.0						
0-7.5					19.2		
0-8		26.6	19.2			17.7	15.2
0-9				19.1			
3			16.0				
5		30.0					
6		33.0	30.4	19.2	21.4	19.3	14.9
7		32.5	37.0	19.8	19.9	38.9	35.8
8	58.5	46.6	56.2	23.6	23.8	60.0	37.4
9		44.2	53.6	42.0	50.0	66.6	59.2
10	78.5	39.1	63.2	65.2	64.1	85.5	83.1
11	100.4	39.8	66.0	95.6	117.6	139.1	146.6
12	124.8	47.7	97.0		142.8	170.0	

Table 34. Vertical profiles of total phosphorus (mg/m³) at Hasse Lake, 1982.

	Date							
Depth	5/11	5/31	6/15	7/6	7/27	8/17	9/7	9/27
0–4.5								21.5
0–6		31.9				20.0		
0–6.5					18.8			
0–7	39.1		28.9	27.3			17.7	

Table 35. Vertical profiles of total phosphorus (mg/m³) at Lessard Lake, 1982.

	Date						
Depth	5/25	6/9	6/21	7/12	8/3	8/24	9/13
0-3			20.4			28.9	33.4
0-3.5					31.2		
0-4	41.0	28.7		24.7			

Table 36. Vertical profiles of total phosphorus (mg/m³) at Mink Lake, 1982.

	Date						
Depth	5/11	5/31	6/15	7/6	7/27	8/17	9/7
0–3						77.7	61.3
0–5					31.9		
0–6		32.0					
0–7	54.1		27.1	35.7			

Table 37. Vertical profiles of total phosphorus (mg/m³) at Peanut Lake, 1982.

	Date						
Depth	5/25	6/9	6/21	7/12	8/3	8/24	9/13
0–4	29.3	19.4	18.3		18.6	17.5	
0–6				20.8			
0–7.5						20.5	
0–8	31.9	30.9			21.5		18.5
0–9			26.5				
2		23.8					
4			20.6				
5		32.5			21.8		19.6
5.5				23.3			
6		43.2		23.4	23.5	30.3	17.5
6.5				28.4			
7		50.8	55.2	42.9	47.2	40.6	21.2
8		57.5	57.7	61.6	67.2	54.4	54.9
9		40.8	52.0	68.4	85.1	85.8	97.0
10		38.6	51.2	76.0	97.5	128.0	117.1
11		38.9	59.7	96.1	113.5	138.3	149.7
12		39.4	60.9	103.5	120.7	146.9	187.2

Table 38. Vertical profiles of total phosphorus (mg/m³) at Sauer Lake, 1982.

	Date						
Depth	5/12	6/1	6/22	7/13	8/4	8/23	9/14
0–1	41.8						
0–4		25.5	19.7	18.4	22.2	16.6	
0–6	56.6			19.9			
0–7		36.6					
0–7.5					24.8		17.7
0–8			33.4			23.0	
3			19.6				
5	38.4	45.5		21.6	23.3	19.7	18.9
6		42.0	43.7	25.2	24.8	22.2	18.8
7	44.8	67.0	90.6	60.5	38.4	30.6	34.6
8		63.8	68.0	95.4	119.8	119.1	84.5
9	48.9	65.3	76.0	86.1	91.6	75.8	120.0
10		63.8	75.4	79.8	77.2	87.8	152.0
11	42.2	64.4	69.4	147.6	166.5	207.5	272.9
12		75.8	83.0	187.1	236.1	319.5	350.5

Table 39. Vertical profiles of total phosphorus (mg/m³) at Twin Lake, 1982.

	Date					
Depth	5/26	6/14	7/5	7/26	8/18	9/8
0-4	27.4	11.0				
0-5				12.3	10.8	
0-6						9.2
0-7			11.5			
0-8	31.5					
0-9		13.3			9.9	
9	50.4	46.7	37.4		16.3	22.1
11	48.0	48.0	48.2	50.5	47.6	43.2
13	47.8	44.5	48.4		49.7	52.9
15	52.5	46.8	49.7	59.1	58.2	56.5
17	56.4	52.4	53.5	62.8	74.6	69.5
19	65.2	60.0	67.1		96.1	82.4
20	65.6		69.8		93.0	
21	68.9	67.9	74.7	84.2	99.7	103.9
22	66.6		90.5	91.3	114.3	105.9
23	76.1	77.8	90.1		126.3	112.6
24	81.0		93.9	104.0	128.2	116.0
25	93.4	82.4	103.7	113.2	136.8	143.5
26	92.6		113.6		138.2	173.2
27	112.5	97.5	117.2	145.4	141.3	178.2
28	109.3		129.0		148.9	
29	115.4	104.5	144.0	169.0	174.7	190.4
30	118.4	112.0			187.8	

Table 40. Vertical profiles of total phosphorus (mg/m³) at Wizard Lake, 1982.

	Date						
Depth	5/26	6/14	7/5	7/26	8/18	9/8	9/27
0-2.5						66.9	
0-3				52.5	55.2		57.5
0-5	49.1		46.0				
0-6		35.4					

Table 41. Average chlorophyll *a* (mg/m³) in the euphotic zone of 12 study lakes for each sampling date in 1982.

Lake	Date or Chl *a*								
Amisk N.	Date	5/17	6/7	6/28	7/19	8/9	8/31	9/20	
Amisk S.	Chl *a*	19.0	6.8	6.7	6.9	12.1	12.8	16.0	
	Chl *a*	19.6	7.7	7.8	19.2	13.4	13.4	13.9	
Baptiste N.	Date	5/8	6/8	6/29	7/20	8/10	9/1	9/21	
Baptiste S.	Chl *a*	45.7	9.0	15.2	14.1	31.2	12.3	21.7	
	Chl *a*	44.3	8.6	16.4	3.8	22.5	10.7	11.9	
Eden	Date	5/12	6/1	6/22	7/13	8/4	8/23	9/14	
	Chl *a*	11.8	7.2	3.4	3.4	3.4	3.2	3.0	
Hasse	Date	5/11	5/31	6/15	7/6	7/27	8/17	9/7	9/27
	Chl *a*	9.6	8.0	5.0	5.7	2.9	2.8	2.5	4.9
Lessard	Date	5/25	6/9	6/21	7/12	8/3	8/24	9/13	
	Chl *a*	25.3	6.8	2.9	10.0	15.6	20.3	23.2	
Mink	Date	5/11	5/31	6/15	7/6	7/27	8/17	9/7	
	Chl *a*	11.5	2.4	2.0	6.1	9.6	30.6	23.3	
Peanut	Date	5/25	6/9	6/21	7/12	8/3	8/24	9/13	
	Chl *a*	6.8	5.9	6.2	10.7	4.2	4.7	3.3	
Sauer	Date	5/12	6/1	6/22	7/13	8/4	8/23	9/14	
	Chl *a*	16.1	7.9	4.1	4.5	2.6	5.4	2.7	
Twin	Date	5/26	6/14	7/5	7/26	8/18	9/8		
	Chl *a*	3.7	1.5	1.0	1.6	1.4	1.1		
Wizard	Date	5/26	6/14	7/5	7/26	8/18	9/8	9/27	
	Chl *a*	19.6	6.4	4.6	18.3	24.2	28.0	23.1	

Table 42. Average total nitrogen (TN [mg/m³]) in the euphotic zone of 12 study lakes for each sampling date in 1982.

Lake									
	Date	5/17	6/7	6/28	7/19	8/9	9/20		
Amisk N.	TN	779.1	1069.2	971.4	1140.8	1066.7	1064.3		
Amisk S.	TN	787.7	1035.6	934.3	1044.7	1044.8	1212.3		
	Date	5/18	6/8	6/29	7/20	8/10	9/21		
Baptiste N.	TN	1133.8	1102.6	1187.6	1422.3	1458.4	1443.6		
Baptiste S.	TN	1164.9	1075.8	1249.8	1205.0	1318.9	1097.9		
	Date	5/12	6/1	7/13	8/4	8/23	9/14		
Eden	TN	873.9	511.7	634.2	551.6	628.2	823.3		
	Date	5/11	5/31	6/15	7/6	7/27	8/17	9/7	9/27
Hasse	TN	1320.6	1289.0	1287.4	1245.5	1210.6	1120.8	1315.8	1258.3
	Date	5/25	6/9	7/12	8/3	8/24	9/13		
Lessard	TN	1278.4	1245.0	1203.3	1547.1	1379.6	1922.4		
	Date	5/11	5/31	6/15	7/6	7/27	8/17	9/7	
Mink	TN	1391.3	1063.3	1153.2	1140.3	1160.7	1345.3	1562.7	
	Date	5/25	6/9	7/12	8/3	8/24	9/13		
Peanut	TN	1328.5	1371.9	1379.0	1599.1	1593.4	1378.0		
	Date	5/12	6/1	7/13	8/4	8/23	9/14		
Sauer	TN	1282.1	1161.6	1073.0	1040.5	1059.4	1324.5		
	Date	5/26	6/14	7/5	7/26	8/18	9/8		
Twin	TN	322.3	309.9	277.6	316.7	269.3	330.4		
	Date	5/26	6/14	7/5	7/26	8/18	9/8	9/27	
Wizard	TN	1104.3	1037.3	999.5	1182.2	1371.4	1485.8	1223.6	

Table 43. Zooplankton species found in select samples from 19 lakes in central Alberta. Relative abundance is indicated by a scale which ranges from very common (++++) to rare (+). A ? indicates uncertainty about species identification.

Lake	Date	Species	
Amisk N.	9/8/82	*Daphnia galeata mendotae*	+
		Diaphanosoma leuchtenbergianum	+
		Diaptomus oregonensis	++++
		Cyclops vernalis }	++
		Mesocyclops edax }	
Amisk S.	13/7/81	*Daphnia galeata mendotae*	++++
		Daphnia pulicaria	++
		Leptodora kindtii	+
		Diaptomus siciloides	++++
		Cyclops vernalis	++
	9/8/82	*Daphnia* sp.	+
		Diaptomus oregonensis	++
		Macrocyclops albidus	++
Baptiste N.	10/8/82	*Daphnia galeata mendotae*	++++
		Leptodora kindtii	+
		Diaphanosoma leuchtenbergianum	+
		Diaptomus oregonensis	+++
		Mesocyclops edax	++
		Chaoborus sp.	+
Baptiste S.	14/7/81	*Daphnia galeata mendotae*	++++
		Diaphanosoma leuchtenbergianum	+
		Leptodora kindtii	+
		Diaptomus oregonensis	+++
		Cyclops vernalis }	+++
		Mesocyclops edax }	
	1/9/82	*Daphnia galeata mendotae*	++++
		Daphnia sp. (*pulex*-type)	+
		Diaphanosoma leuchtenbergianum	+
		Ceriodaphnia lacustris	+
		Leptodora kindtii	+
		Diaptomus oregonensis	+++
		Mesocyclops edax }	++
		Cyclops bicuspidatus thomasi }	
Birch	22/6/81	*Daphnia pulicaria*	+++
		Diaptomus oregonensis	+++
		Cyclops bicuspidatus thomasi	+++
		Ceriodaphnia sp.	+
		Chaoborus sp.	+
Eden	6/7/81	*Daphnia thorata ?* •	+++
		Ceriodaphnia lacustris	++++
		Diaptomus oregonensis	++
		Cyclops bicuspidatus thomasi	+
		Chaoborus sp.	+

continued ...

Table 43. continued

Lake	Date	Species	
Eden	23/8/82	*Daphnia galeata mendotae* ?	++++
		Ceriodaphnia lacustris }	++
		Ceriodaphnia reticulata }	
		Diaptomus oregonensis	++
		unidentified *cyclopoid*	+
Hasse	24/6/81	*Daphnia pulicaria*	++++
		Diaptomus oregonensis	+++
		Cyclops bicuspidatus thomasi }	++
		Mesocyclops edax }	
	6/7/82	*Daphnia laevis* #	++++
		Ceriodaphnia acanthina }	+
		Ceriodaphnia lacustris }	
		Diaptomus oregonensis	++
		Bosmina longirostris	+
		Diaphanosoma leuchtenbergianum	+
		Mesocyclops edax }	+
		Cyclops vernalis }	
		Chaoborus sp.	+
	17/8/82	*Daphnia galeata mendotae*	++++
		Diaptomus oregonensis	++
		Mesocyclops edax	+
Hastings	10/7/81	*Daphnia schodleri*	++
		Diaphanosoma leuchtenbergianum	+
		Diaptomus siciloides	++++
		Cyclops vernalis }	+
		Cyclops bicuspidatus thomasi }	
Hubbles	24/6/81	*Daphnia pulex* -	++++
		Ceriodaphnia sp.	+
		Diaptomus oregonensis	+
		Macrocyclops albidus	+
		Chaoborus sp.	+++
Lessard	3/8/82	*Daphnia galeata mendotae*	++++
		Ceriodaphnia lacustris	++++
		Diaphanosoma leuchtenbergianum	+
		Diaptomus oregonensis	++
		Mesocyclops edax	++
		Chaoborus sp.	+
Mink	23/6/81	*Daphnia galeata mendotae* }	+++
		Daphnia laevis }	
		Diaptomus oregonensis	++++
		Cyclops bicuspidatus thomasi	++

continued ...

Table 43. continued

Lake	Date	Species	
Mink	17/8/82	*Daphnia galeata mendotae*	++
		Diaphanosoma leuchtenbergianum	++
		Ceriodaphnia lacustris	++++
		Bosmina sp.	+
		Diaptomus oregonensis	++++
		Mesocyclops edax	++
Nakamun	22/6/81	*Bosmina longirostris*	++++
		Acanthodiaptomus denticornis	++++
		Diaptomus oregonensis	
		Mesocyclops edax	++
		Cyclops vernalis	
Narrow	27/7/81	*Daphnia pulicaria*	++++
		Diaptomus oregonensis	+
		Mesocyclops edax	++
		Cyclops bicuspidatus thomasi	
		Chaoborus sp.	+++
Peanut	3/8/82	*Daphnia galeata mendotae*	+++
		Diaptomus oregonensis	+++
		Diaphanosoma leuchtenbergianum	+
		Ceriodaphnia lacustris	+
		Bosmina longirostris	+
		Cyclops bicuspidatus thomasi	++
		Mesocyclops edax	
		Chaoborus sp.	+
Roi	17/6/82	*Daphnia pulicaria*	++++
		Diaphanosoma leuchtenbergianum	+
		Acanthodiaptomus denticornis	++
		unidentified *cyclopoid* (immature specimens only)	+
		Chaoborus sp.	+
	24/8/82	*Bosmina longirostris*	++
		Diaphanosoma leuchtenbergianum	+
		Diaptomus oregonensis	+++
		Acanthodiaptomus denticornis	
		Orthocyclops modestus	+
		Chaoborus sp.	+
Sauer	30/6/81	*Daphnia galeata mendotae*	+++
		Daphnia pulicaria	+
		Leptodora kindtii	+
		Diaptomus oregonensis	++
		Mesocyclops edax	++++
		Cyclops bicuspidatus thomasi	
	23/8/82	*Daphnia galeata mendotae*	+++
		Diaptomus oregonensis	+++
		Cyclops bicuspidatus thomasi	+
		Mesocyclops edax	

continued ...

Table 43. Concluded.

Lake	Date	Species	
Star	23/6/81	*Daphnia pulicaria*	++++
		Diaptomus oregonensis	++
		Cyclops bicuspidatus thomasi }	+++
		Mesocyclops edax }	
Twin	1/7/81	*Daphnia pulex*	++++
		Diaptomus leptopus	+++
		Cyclops bicuspidatus thomasi	+
		Chaoborus sp.	+
	18/8/82	*Daphnia pulicaria*	+++
		Diaptomus leptopus	+++
		Cyclops vernalis	++
		Chaoborus sp.	+
Wizard	1/7/81	*Daphnia galeata mendotae*	++++
		Diaptomus oregonensis	+++
		Acanthodiaptomus denticornis	+
		Leptodora kindtii	+
		Mesocyclops edax }	++
		Cyclops bicuspidatus thomasi }	
	18/8/82	*Daphnia retrocurva*	++
		Leptodora kindtii	+
		Diaptomus oregonensis	+
		Mesocyclops sp. ?	++

* Not supposed to occur here, according to Brooks.
# Tentatively identified by Arni Litt, but not supposed to occur in Alberta according to Brooks. Similar-looking to some of what I have called *galeata mendotae*.
- Distinction between *pulex* and *pulicaria* is subjective.